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Contributions to the Synanthropic (Adventive) Flora of the Railroads in St. Louis, Missouri, U.S.A. *Viktor Muhlenbach* 1

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CONTRIBUTIONS TO THE SYNANTHROPIC (ADVENTIVE) FLORA OF THE RAILROADS IN ST. LOUIS, MISSOURI, U.S.A.

VIKTOR MÜHLENBACH[1]

ABSTRACT

Based on 563 excursions from 1954 to 1971, 393 synanthropes (adventive plants not native to the flora of Missouri) were discovered on the railroad network in St. Louis. The majority were weeds and escapes from cultivation. The plants belonged to 59 families. The best represented families were Gramineae (74), Compositae (52), and Cruciferae (28). During this study 129 new taxa to the flora of Missouri were discovered of which 39 taxa are reported for the first time in this paper. The results of this study are quite similar to comparable European studies. There was a preponderance of annuals (254 of 393); most species were rare (208 were deemed very rare—no more than 5 localities in 18 years); the majority of plants were ephemeral (47 were seen only once as a single plant, 52 were seen only as a single colony); and there is much fluctuation in the frequency of most species. Eighty-nine species were considered to be naturalized. Other characteristic features of these railroad plants were nanism and seed dormancy. It was not possible to determine the exact means of introduction for the great majority of synanthropes. Many synanthropes were found along classification or switching tracks in freight yards, fewer along trunk lines. The habitat preferences and gregarious behavior of various species is discussed. The most common synanthropes were: *Bromus tectorum*, *Digitaria sanguinalis*, *Setaria viridis*, *Kochia scoparia*, *Amaranthus retroflexus*, *Capsella bursa-pastoris*, *Melilotus officinalis* and *Convolvulus arvensis*. Native species were studied also, but in less detail. Some of the most common native species were: *Eragrostis pectinacea*, *Hordeum jubatum*, *Aristida oligantha*, *Lepidium virginicum*, *Euphorbia dentata*, *Erigeron canadensis*, *Ambrosia artemisifolia* and *Helianthus annuus*. The devastating effect of the extensive use of weed killers in modern railroad management on railroad plants is discussed.

Since 1954 I have been working on the adventive flora of the railroads of St. Louis. These studies followed similar studies in my native city, Riga, Latvia, where I observed the adventive flora of the railroads for 20 years (1924–1944). Results for the first half of this period (1924–1932) were published (Mühlenbach, 1927, 1932–1934). During these years 128 species were found which were not native to Latvia—they were introduced by the railroads. The extensive material collected during the second half of this period was lost during World War II, and remains unpublished.

The St. Louis metropolitan area has a railroad network that is the second largest in the United States. It seemed that a study of the presence, frequency, and ability to survive of introduced plants could be rewarding. The railroads

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in St. Louis have never been examined from the botanical point of view, and it soon became obvious after initiating my studies that very little is known about plant life on the railroads for the entire United States. It seems that American botanists have been much more interested in the study of roadside vegetation (see Frenkel, 1970, for a thorough treatment for California). In Europe, on the other hand, numerous papers on the flora and vegetation of railroads, especially the freight and switching yards, have been published. An extensive selection of newer papers on the subject is given by Hamann & Wagenitz (1970) in their bibliography for the *Flora von Mitteleuropa*. Such studies have probably been most thorough in Germany and Switzerland.

Railroads have frequently exerted a strong attraction to many people, and botanists have not been an exception. Experience in many countries has shown that one can easily find numerous rare plants along railroad tracks. My feelings are very much like those of the prolific author of adventive botany, Meyer (1932a), who calls the pursuit of railroad-yard floras one of the most fascinating studies in botany. However, for the sake of fairness, one must acknowledge that there are also opposite views. Müller (1935) writes: "Many botanists consider the pursuit of adventive plants of little value, even a useless waste of time."

Lehmann (1895), one of the first pioneers in railroad botany, called the freight and switching yards "botanical gardens of a kind." The comparison holds to a certain degree. In both places one may find a multitude of rare, strange, and unfamiliar plants; however, the way these plants are perceived and treated in these two places differs enormously. Whereas man exerts the best possible care of the plants in botanical gardens, he usually wages an embittered fight against the plants of the railroads. It is a pity to say that this fight has been constantly increasing in intensity and effectiveness in the last two decades. Another difference is that man, as a rule, brings plants to a botanical garden intentionally, while the plants on railroads move in on their own without the wish or even knowledge of man. These plants hitchhike, so to speak, becoming attached in one way or another to the freight or, in rare cases, the rolling stock of the trains.[2]

REVIEW OF LITERATURE

Linnaeus already recognized the role of trade and traffic in the dispersal of plants. Flygare (1768) in the *Amoenitates Academicae* discussed the dispersal of seed. Seven different means of dispersal were described, the last one being commerce. In Linnaeus's time two main ways existed for spreading seeds through commerce. Many goods might contain the fruits, seeds, or other parts of plants suitable for propagation. Agricultural products such as cereals, wool, cotton, and oil seeds are especially likely to contain such plant propagules as impurities. The second main way of spreading plants by commerce was through use of ballast by seagoing ships. Ballast often consisted of earth, rocks, or sand. This would often be shifted from one harbor to another as needed and the same material might easily travel to many different parts of the world. Considering the material most often used as ballast, it is no wonder that it often contained fruits, seeds,

[2] Levina (1944) called this process agestochory (from the Greek—to convey or to transport by themselves).

rhizomes, bulbs, etc. Consequently rich "ballast floras" frequently developed and many "ballast plants" were widely distributed in many countries.

In the United States, beginning in 1864, the flora of the harbor and its ballast grounds were examined especially carefully in Philadelphia, and on the opposite shore of the Delaware River in New Jersey. Extensive lists of introduced plants were published by Smith (1867), Martindale (1876), and Burk (1877). Smith discovered 106 introduced plants in 3 years and Burk added 125 more species. With even bigger success Brown (1878) began in 1877 to study the ballast flora of wharves and abandoned overgrown ballast grounds in the New York harbor, as well as in similar localities along the Hudson River in New Jersey. Brown's list contained 386, mostly European, species. He maintained that the large number of ballast plants was caused by the continued large balance of trade in favor of the United States. Therefore, many more ships unloaded ballast than took on ballast, thereby increasing the chance for adventive plants to establish themselves. It is very interesting that besides giving their lists, American botanists mentioned some features and pecularities of the ballast flora which were much later discovered anew and described by railroad botanists in Europe. Smith (1867) transplanted juvenile plants threatened by frost so that they could develop flowers and fruit in greenhouses. Burk (1877) observed that many plants exist only one season and then disappear. Brown (1878) observed that species that may remain for years often show strong fluctuations in their numbers from year to year. He also observed (Brown, 1881) that some plants often change their locality and explained their reappearance by newly introduced seeds. Seed dormancy was discovered to be a factor as well—many species suddenly appeared on grounds where ballast might have been deposited as much as four years previously. Fluctuation of species richness due to disturbance by man for business purposes was often an important factor in a ballast flora. Railroads were mentioned in these early ballast studies as well, but only because the ballast there was used as a fill for railroad tracks. No thought was given to the possibility that the railroads themselves might have been a source of introduction of inland plants.

In the second half of the 19th century, railroads began to develop. Also, ships began to use water instead of earth and sand as ballast. This procedure was cheaper, less time consuming, and considerably increased the cleanliness of the ships. It also meant the downfall of the ballast flora everywhere. However, the role of maritime commerce in the introduction of plants did not entirely cease. Transported freight continued to be a vehicle for transporting alien plants. Voyages which begin on a ship are mostly continued on railroads until a final destination point for the goods is reached. However, diaspores may easily escape in a harbor before further transport; therefore, many harbors, both coastal and inland, often contain a sizeable number of introduced plants.

From a botanical point of view, the most famous harbor is Port Juvenal near Montpellier in France. The history of adventive plants in the harbor began in the heyday of the ballast floras but continued into the 20th century. In 1813 de Candolle called the attention of botanists to this place, and many renowned botanists visited it. Thellung (1912, 1915) gave the description of botanical

events in his doctoral thesis. The richness of the flora in alien plants was due to the wool washing establishments there. For a century wool from all over the world was imported and cleaned from impurities that included innumerable seeds and fruits equipped with barbed awns, hooked prickles, bristles, etc.

Thellung analyzed the previously published lists and found that beginning in 1815 Oriental plants were exclusively represented. A little later Algerian plants appeared. Around 1830 the first South American plants arrived, and in 1870 Australian plants appeared. It was thus possible to reconstruct the commercial history of the wool washing establishment from botanical observations. Many introduced plants were discovered and described before they became known in their native countries, and for some, the land of origin is still unknown. Thellung compiled a list containing 800 species—the majority being the wool adventives and most of the others being escaped cultivars.

Another very interesting book dealing with wool adventives was published by Hayward & Druce (1919) based on work from 1907 to 1918. Hayward scrupulously explored the banks of two rivers, Tweed and Gala, into which abundant effluents of woolen mills at Galashiels, Selkirk County, Scotland, were discharged. Other plants were collected from woolen mill refuse heaps and places where the refuse was used as a fertilizer. The writers mentioned the role of the railroad in transporting diaspores in wool but failed to realize that some wool adventives would also have been spread along the railroad itself.

Hayward and Druce enumerated 348 wool adventives and also listed introduced plants which arrived in other ways. Many wool adventives found at Galashiels were recorded for the first time in Europe, and new species were described with origins unknown. In comparison with Montpellier the percentage of Australian, Asiatic, South African and North American species was much higher. The writers emphasized that most of the wool adventives were ephemeral in the Scottish climate so that naturalization rarely took place.

In the beginning of the 20th century, some ballast grounds in the Baltimore harbor area were still present. C. C. Plitt frequently collected there in the years 1900 through 1904 and a partial record of his findings was given by Fessenden (1956). As usual, new species were found but many plants defied determination. In 1953 in Baltimore Reed (1964) begin to investigate the huge piles of chrome ore that were waiting delivery to steel mills. Altogether 536 species of flowering plants were collected, mostly on chrome-ore piles. Many species were natives, but the overwhelming majority were introduced. About 80% were new to Fernald's *Gray's Manual of Botany* or Gleason's *Illustrated Flora of the Northeastern United States and Canada.* There were many African species, particularly among the grasses, which is not surprising since Rhodesia and Ghana are major chrome ore exporting countries. A similar flora occurs in similar situations in the port of Newport News, Virginia and along seven miles of the Chesapeake & Ohio railroad from the harbor inland to where huge piles of different ores have been stocked by an ore refining company.

The botanical investigation of many islands which are accessible only by ships showed that the introduction of plants may play a very distinct, even fatal role for the native vegetation. The most famous example is the island of St.

Helena. The exceedingly interesting native flora of this island, which consisted mostly of endemics, was greatly reduced through competition from imported foreign plants and/or overgrazing from several domesticated animals. Good (1964) cited Melliss (1875) who noted that among 900 species of flowering plants on St. Helena only about 30 were really native. In the Western Hemisphere similar examples abound. For example, Harris (1965) estimated that on Antigua and Bermuda islands 180 out of about 900 flowering plants were introduced. Of course, part of the aliens were brought in deliberately as food crops or ornamentals, but numerous herbaceous weeds and grasses have spread into these islands after their accidental introduction. These examples prove that navigation has played and will continue to play an important role in the dispersal of plants and the introduction of aliens.

Approximately at the same time that the ballast flora began to decline, the era of railroad transportation on the continent began to develop. The first railroad with steam traction was inaugurated between Darlington and Stockton in England in 1825 and served only freight traffic. The first passenger line was also opened in England between Liverpool and Manchester a year later. In 1837 the first lines were opened in Germany and Belgium. In the 1840s railroad construction boomed all over Europe. Curiously, the role of the railroad in the introduction of alien plants was slow to be understood. This is evident from the numerous local floras that were being published by different German botanical and natural historical societies at that time. Rare plants were enumerated and railroad localities were often mentioned. Many plants in those localities were decidedly alien. Nevertheless, in the beginning it occurred to no one that there could be a connection between the railroad operations and the alien plants in the vicinity even though foreign grain, as well as wool, could arrive in most places only by train. Some papers of the famed P. Ascherson showed quite distinctly that it took a long time to solve the question. For example, in 1860 he described the discovery of *Sideritis montana* L. near Magdeburg in the vicinity of a railroad bridge on a moist bank of the Elbe River, together with *Alyssum montanum* L. and *Stachys annua* L. Ascherson attributed their occurrence to alluvium from the river. But as all three plants are inhabitants of dry, rocky habitats, he called this colony's habitat very surprising. No thought was given to the railroad bridge in the shadow of which the plants had grown. Many similar examples could be cited.

Perhaps the very first to unmistakably point to railroads as introducers of alien plants was Kreuzpointner (1876),[3] who accidentally discovered in the Thalkirchen

[3] It appeared for a while that another writer had described the role of railroads considerably earlier. Preuss (1928–1929) described the discovery by Eggemann (1859) of the first wool adventive, *Medicago intertexta* Willd., at a cloth factory at Haste near Osnabrück. According to Preuss, Eggemann stated that it was introduced with wool from Buenos Aires. After studying the original manuscript, it became clear that the sentence "the wool which the new railroad has brought in" was an addition by Preuss himself. Kreuzpointner must still be considered as the first who has clearly recognized and published the role of the railroad in plant introductions. After my manuscript went to press I returned to the German botanical literature preceding 1876 and discovered that several writers before Kreuzpointner pointed out the role of railroads in unintentional introduction of plants. The earliest paper now appears to be the one by Caflisch in 1848.

railroad station near München a "great multitude" of rare plants growing around the municipal warehouses. He enumerated 84 species. In the warehouses immense amounts of Hungarian, Russian, and Italian grain were stored and partly cleaned. There was no doubt that the source of these aliens was the grain. Earlier (1862–1880) Holler made similar observations in Augsburg on a trunk line 25 km long, but he did not publish until 1883. He listed 44 species and recognized that they were introduced by grain transports. He also described some peculiarities which are still valid today. He noted that there was a distinct predilection of many aliens to grow either in the stations or along a trunk line which was double tracked. The aliens were mostly concentrated along the track on which the trains with grain shipments were routed. On the opposite track some aliens were also found, but of a different origin. The preferred location was in curves of the track. He also realized that some aliens were characteristically unicates.

Soon afterwards numerous papers on railroad plants were published. Among this multitude of papers is one by Lehmann (1895; with supplement, 1896) of which the greater part is devoted to the local flora of one of the provinces of Latvia. The chapter on dispersal of plants by railroads was very significant to me for my treatment of the railroad flora in Riga, but, besides this, it contains many observations of general interest. The importance of this treatise was first stressed by another ingenious railroad botanist, Matthies (1925), who emphasized that "strangely enough a comprehensive treatment of this problem in the scientific literature is given in reality only by Lehmann." Lehmann was a physician who traveled extensively on railroads, using even freight trains. Finding the vegetation on the railroad right-of-ways very interesting, he began investigations in the big freight yards in Dünaburg (now Daugavpils). He concluded that it was very important to continuously observe the flora's immigration, perseverance, and disappearance. Lehmann distinguished between railroad plants in a broad and narrow sense. In a broad sense, railroad plants included those from the surroundings. Many native plants were brought in during the construction and maintenance of the embankments and slopes, especially in sod used for erosion control, causing many meadow plants to appear in unusual places. In a narrow sense, railroad plants were those imported or introduced from more or less remote distances. The invasion of railroad plants took place by ballast[4] and maintenance trains, by freight trains, and rarely by passenger trains. Ballast contributed much to the invasion of alien plants. After investigation of the flora of different sand and gravel pits from which the railroad took the ballast, Lehmann could in many cases reveal, to the surprise of officials, where the ballast originated.

Lehmann (1895, 1896) also noted that plants are generally dispersed by freight trains carrying grain. Such grain is never free from weed seeds, whether transported in sacks or in bulk. The small weed seeds which are usually heavier may sift through the grain and fall to the ground through cracks in the freight cars. Lehmann once observed this with flax, finding small sturdy specimens of

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[4] Ballast as used here has nothing to do with ship ballast. Railroad ballast consisting of sand, grit, cinder, gravel, and crushed stones is intended to prevent the shifting of the cross-ties and to increase the solidity of the tracks.

flowering flax standing parallel to the rails for 2 km. Besides grain and flax, the transportation of all kinds of produce and livestock could be effective in distributing seeds.

Switching and freight yards and, to a lesser degree, trunk lines can yield a rich flora of adventives unless the railroad management is very tidy. In large freight yards there are usually little-used tracks with wide intervals between the tracks and open plots where weeding is not taken too seriously and where introduced seeds may flourish. Lehmann noted that the older the railroad, the larger the colonization by alien plants, especially of the subboreal type.

The dispersal of plants by passenger trains occurs when seeds arrive with the luggage or in the packing material of easily perishable goods which require shipping on more rapid passenger trains. The presence of an alien growing at that time as a frequent ornamental in gardens along a trunk line gave Lehmann the idea that it owed its existence to a discarded bouquet of flowers.

Lehmann (1895–1896) considered the difficult question of when one may claim naturalization of an introduced plant. Klinggräff (1866) had suggested that a period of 30 years should be demanded before a plant is considered naturalized. In many cases Lehmann believed such an interval to be unnecessarily long, but in other cases not long enough for actual naturalization.

Approximately at the same time, Huth (1895) described an unusual experiment done in the surroundings of a supply depot connected with a large military bakery and granary in Frankfurt-an-Oder. Here rye from southeastern Europe, Hungary, and South Russia was ground. The chaff left over after the cleaning of the rye was repeatedly scattered over four grass plots of the supply depot. For many years different adventives were found in these plots.

In the beginning of this century an intensive study of plant introduction was started by Thellung in Switzerland. In 1905 he published statistics which revealed how profoundly railroads, which were the only means of importing goods into Switzerland, had contributed to the introduction of adventives. He recorded 1,049 ruderal and adventive species in the canton of Zürich. In the Zürich station and nearby gravel pits alone, 769 species were recorded. Of these, 318 species were native to Zürich (apophytes), 104 species were escapes from cultivation (ergasiophygophytes), 150 species were naturalized in Zürich from foreign origin including prehistoric weeds (archaeophytes), and 196 species were transient (ephemerophytes). In 1911 Thellung noted that many Mediterranean and American species that were known to be naturalized in Australia were introduced into Switzerland from Australian wool. In 1919 he termed this phenomenon secondary introduction. In this same paper, he noted that many Mediterranean species were being introduced with hay that was used as the packing material for southern citrus fruits.

In 1905 Hesselman edited the paper of the late Swedish botanist Sternstroms who had compared both slopes of the embankments of one Norwegian and 11 Swedish railroads from the ecological point of view, noting the importance of unequal solar irradiation.

Zimmermann in 1907 published a book on the adventive and ruderal flora of Mannheim, Ludwigshafen, and the Palatinate (Pfalz). Zimmermann worked for

decades and brought together huge amounts of material so that knowledge of the Mannheim adventive flora remained unsurpassed in Germany. A criticism of Zimmermann was that the localities are not sufficiently pinpointed, making it difficult to estimate what agent had caused the dispersal of the adventives—the harbor on one side or the nearby railroad and freight yards on the other side. Zimmerman thought that cereal grains unloaded in Mannheim were the most important vehicle for adventives. Most adventives were annuals that frequently did not develop seeds for lack of pollinating insects. He also found that many seeds did not germinate at all. Then he discovered that in some cases the railroad cars themselves, not the freight, were the source of the adventives, finding alien seeds in the sweepings of the roofs or cars which arrived from abroad.

Another writer, Schnyder (1910, 1914), who was the stationmaster of the Swiss railroad border station Buchs, was able to observe the vegetation in his station the year around. Schnyder discovered numerous plants which had arrived in the Buchs station as stowaways. He was convinced that the expansion of plant ranges resulted from railroad introductions, not the unaided natural dispersal of the plants themselves. The föhn wind of the Alps dispersed the seeds widely in the area. Many plants did not survive because the climate did not suit them, but many of them were reintroduced again and again. Some of the adventives found their way into the villages as grain refuse sold as feed for fowl.

During World War I Schnyder pursued interesting observations on the importance of the source of freight in introducing different adventives. Transports between Italy and Austria were of two kinds: letters and parcels for the Italian prisoners of war and citrus fruits which Italy continued to sell to Austria. Both shipments arrived in separate freight cars and were unloaded on different tracks. In the following season the citrus transports had introduced almost entirely Mediterranean weeds which were previously recognized in Zürich by Thellung as associates of citrus fruits. Around the unloading sites of the mail only cultivars were present. Schnyder also confirmed Thellung's opinion that an increased growth follows weeding because the break-up of the soil creates improved conditions for germination.

Matthies (1925) did his doctoral dissertation research on the significance of the railroad for the dispersal of plants in Mecklenburg. He frequently cited the conclusions of Lehmann (1895), but he was less interested in the synanthropes than in the vegetation of the railroads as a whole. From a botanical standpoint he examined, in great detail, the importance and influence of the so-called fixed properties of the railroad: the slopes of the dams or banks and cuts, the embankments of the tracks, and the stations or yards, considering the effects of factors such as topography, construction methods and materials, maintenance procedures, and fires in the establishment, succession, and persistence of plants. Matthies discovered that under telegraph wires, which in general accompany railroads, bird-dispersed (endozoic) plants were frequently found. Seeds fall to the ground in the droppings of numerous birds which use wires as a resting place.

Matthies accepted Lehmann's views that freight trains were by far the most important cause for introductions. However, he discovered an important side

effect of high speeding passenger trains, namely, the formation of whirlwinds with suction effects that are effective in spreading diaspores.

Matthies also examined the controversial question of whether the weeding on the railroad was advantageous or harmful for an adventive flora. Lehmann (1895) had concluded that the adventive flora would be more abundant without weeding and that adventive plants receded to little used tracks. Thellung (1915) concluded the opposite. He found that luxuriant, undisturbed vegetation was composed of the most common species, while the scanty starts of reestablishing growth after weeding revealed the most interesting aliens. Matthies confirmed that in Mecklenburg the circumstances described by Thellung were also valid.

After World War I, thorough investigations of several large freight yards were made by German botanists. Until then only one large German freight yard, the München-Süd, had been botanically well investigated. The results were not separately published, but numerous findings were included in Vollmann's (1914) *Flora von Bayern*. Scheuermann (1930), during a period of six years, explored a large number of freight yards, mainly the Dortmund-Süd and Düsseldorf-Derendorf, as well as the inland harbor of Düsseldorf in the Rhenish-Westphalian industrial region. He and his collaborators collected almost 270 Mediterranean, about 60 American, and about 20 East European species. These findings showed that in this region the predominant agent in the introduction of alien plants, the Russian and Hungarian grain, played a lesser role than previously in Germany. Scheuermann pointed out that the vast preponderance of Mediterranean plants was due to the huge import of Italian citrus fruits. Sicily could be pinpointed as the main supplier. Many weeds of these warmer regions succeeded in adhering to the packing material of these fruits. Dr. Markgraf (pers. comm.) has suggested that this distinct group of introduced plants be called "citrus weeds."

Scheuermann discovered early that a surprising conformity of the alien floras existed in different German and Swiss railroad yards of the industrial region, even with regard to the frequency of appearance of single species. Three more categories, oil producing seeds and fruits, bird seeds and their associates, and citrus weeds, were added by Scheuermann to Thellung's (1919) system of introduced plants, which included: grain weeds, wool plants, ballast plants in harbors, and plants introduced by transport vehicles.

Scheuermann was primarily interested in the citrus weeds, but admitted that in some cases Mediterranean plants could be brought in by other goods and dirty cars. The citrus weeds appeared in great numbers around the unloading sites where many germinated and matured. There were species that did not miss a single year; others might fail one year, but reappear, all the more numerous, another year. As a rule, the great majority of citrus weeds showed up as few specimens and frequently as unicates. Scheuermann considered that not all alien plants were introduced by railroads but gained ground on suitable railroad soil by natural ways. He called them migrant plants. Scheuermann stated, "They are absent along the unloading sites where they have to be present if they were introduced by railroad goods." He also noted that not all introduced citrus weed seeds germinated. It was possible to collect many fruits of a *Medicago* species, however, the plant was never found.

Scheuermann had no doubt that many native German plants that had been naturalized in Italy were reintroduced into Germany with the citrus weeds along the unloading sites. He also began to recognize a serious danger to railroad plants, when the German railroads put special weed killing or spray cars in service. This greatly decreased the yield of plants. The same was beginning to happen in Switzerland. He believed that one of the most important problems to be solved was the clarification of which species were not introduced by the railroad but immigrated by themselves. This topic was discussed in more detail by Scheuermann & Krüger (1933).

Scheuermann in 1934 and 1940 returned to citrus weeds and included quite a few species which previously had defied determination. Reintroductions were observed frequently. Scheuermann also examined the effect of packing material in the manner done by Meyer (1931) and explained why many plants whose diaspores are found in packing hay were missing in the yards as living plants. Aquatic and marsh plants naturally could not be found in the yards and perennials were confronted with unfavorable local conditions, especially winter frost. Annuals were less handicapped. A closer examination of the packing hay partly explained the difference in dispersal of the citrus weeds. Plants and inflorescences that easily broke in pieces and fruits that allowed seeds to drop out appeared in yards and, to a lesser degree, on dumps. On the contrary, plants with very tough inflorescences or those in which the fruits firmly adhered to the stem were more likely to be found on dumps and seldom in yards. Scheuermann also found that an extraordinary disparity existed between the numerous introduced fruits and seeds and the number of individuals which appear as living plants. For each living specimen there were hundreds of fruits and seeds.

Bonte (1930) in his investigations for the period 1909–1927 covered the Rhenish-Westphalian industrial region. He frequently collaborated with Scheuermann, but also had other coworkers. The main difference was his approach to the problem. In contrast to Scheuermann, who confined himself to the adventive flora of the freight yards, Bonte extended the search to wherever adventives could be found. It was clear for him that railroads and ships brought in most of them on the manifold goods, fruits for direct consumption, and grain, oil fruits, and wool for processing before final use. Therefore, he directed his attention to the courtyards and adjacent lots of different manufacturing works, mills, and factories. He and his coworkers recorded 711 species.

His remarks about the influence of World War I were very interesting. In 1913, when trade and traffic were prospering with the import of foreign goods, a rich adventive flora had developed in the harbors, freight yards, and dumps. Then in 1914 the war began and every conveyance from foreign countries ceased. The number of aliens abated quickly. By 1916 almost nothing was left in places were aliens previously introduced with grain, oil fruits, wool, and other goods had thrived in abundance. After 1920 the number of alien plants began to increase yearly. In 1937 a new approach was begun by Bonte's coworker, Woermann, in Dortmund. He planted the sweepings from a Sicilian freight car which had been used in the transport of citrus fruits. He succeeded in raising in the garden a dozen different species which were potential citrus weeds. The total

sum of adventives now reached 980 in the industrial region, but as mentioned before, this number included many natives which were considered to be introduced in the yards.

Meyer (1930, 1931) published papers on the freight yards of Breslau and its surroundings. Meyer was the first to record the entire vegetation of the yards, not just the adventives. Altogether 480 species were recorded, not counting obviously planted species. Weed killing, which had a disastrous effect on the vegetation of the yards, was now becoming quite common, leaving large sections of the tracks almost bare of vegetation. However, some unloading sites showed abundant vegetation around the buffers and on some green ruderal strips which were also included in his investigation.

In 1931 Meyer reported on the citrus weed question once more in great detail, after carefully observing the hay and straw used for packing, and established that the manner of handling and disposal of this material corresponded with the appearance of adventives. As many as 73 species were isolated from the hay of a single car.

Differing from the previous authors who frequently observed and collected plants in railroad yards for years, Meyer (1932, 1933a, 1933b) published his observations in speedy succession. Different questions were stressed, but a basic emphasis was always the determination of the kind of imported goods, with which the aliens had been introduced. But he admitted that not every species could be positively attributed to one of the seven groups of adventive plants of Scheuermann and considered the clarification of this question to be the most important problem of the railroad botanist. He also transplanted plants which did not manage to flower out-of-doors to a greenhouse so that they could be identified.[5]

Meyer (1937) described in detail the experiments of Johannes Spethmann who sowed residues from different imported cereals, separating them according to their provenance. The experiments showed that Moroccan barely contained seeds of a multitude of citrus weeds, but in this case introduced without doubt by barley. It clearly indicated the difficulty of assigning each adventive to a particular introduction group. Meyer also advised that it is sometimes very profitable to remove large plants from places where adventives could be expected so that they might not be suppressed from competition.

Probst (1933) published a compilation of his previous papers on the adventive flora of the Swiss canton Solothurn. Only 30 railroad plants were perfunctorily treated but adventives of three large processing factories were discussed in greater detail: 460 wool adventives, 85 cotton adventives, and 300 malt and oat adventives were found.

Hupke (1935, 1938) published reports on adventive plants in the freight yards, inland harbor installations, and dumps in Cologne, especially stressing the erratic appearance of adventives and their dependence on new introductions into the yards.

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[5] Thellung (1915) gave this same advice, but the very first who applied this method was A. H. Smith (1867) in Philadelphia.

Müller (1935) demonstrated that opportunities exist for an adventive botanist if systematic work is done at the right time and in the right place. Until 1910 only 60 adventive species were recorded from the state of Württemberg in southwest Germany. Müller was able to compile a list of 280 species from 1931 through 1934 with the help of six coworkers. Like his predecessors he tried to determine the manner of introduction. It was not always possible, but he stressed two points: the study of the habitats where the plants were found and the unselfish cooperation of botanists.[6]

Müller concluded that some adventives were introduced in several ways. Citrus weeds had to be recognized sometimes as wool adventives or even as birdseed weeds. He also supported the opinion of Scheuermann that it was necessary to distinguish migrant plants from introduced ones. Migrant plants were missing along the unloading tracks, but were spread in the yards by natural means. In four years about 250 species of hay weeds were found, 150 alone in Ulm, the principal place of his investigation. He also discovered a new introduction medium, cork, with which two Mediterranean plants were introduced into a manufacturing factory's yard.

Müller (1950) continued his research in the last years of World War II until 1948. With the start of the war the number of citrus weeds and woolen weeds began to dwindle rapidly, although not entirely. Apparently some stragglers continued to germinate after a period of dormancy. Aliens were also introduced by cattle and horse transports during the war. Altogether 38 species were counted in Ulm. According to Müller, migrant plants flourished during the war because care of the tracks and installations was limited and weed killing with chemicals did not occur. The migrant plants not only increased in numbers, but also migrated to new localities. New species had even appeared. It was astonishing that it happened in a time when the import trade had completely stopped. Several North American *Lepidium* species traveled along the trunk lines from one station to another. Very little was found after the war; since 1946 only 11 new adventives were discovered, 5 of them considered to be migrant plants.

Laus (1936) published a preliminary report on the railroad flora of Moravia, Czechoslovakia. In general, he found the railroad flora to more or less match the Moravian ruderal flora.

Fiedler (1937) studied another habitat for citrus weeds, namely the Great Central German Produce Market in Leipzig. The total terrain of the market was 16.2 hectares with 11 km of railroad tracks. Such a market assumes to a certain extent the functions of a railroad yard. From 1932 to 1936, 102 species, including a few rare natives, were found. Among them 95 were Mediterranean and could be considered citrus weeds. In Leipzig the most productive packing material was hay. Altogether 371 species, including many Leipzig natives, were isolated from the packing material of the citrus fruits during four winters. Fiedler compared all published material and found that 149 more species were found elsewhere. The total number of citrus weeds in the packing material found in Germany up

[6] The cooperation of the adventive botanists in Germany was very close in the 1930s. As acknowledged in their papers, they exchanged results and literature, collected plants, and permitted the use of unpublished manuscripts.

to that time was 520. In 1935 Scheuermann's coworker, Woermann, was able to grow 70 species from the packing hay gathered in Leipzig. Several had never been observed before. All other foodstuffs arriving in Leipzig added practically nothing to the adventive flora of the market.

Fiedler published (1944b) further developments in the adventive flora of the Produce Market for the years 1937–1942. After the outbreak of World War II, the import of southern fruits was greatly reduced; nevertheless, numerous southern plants appeared again and again around the loading sites. The sum of observed adventives was raised from 102 to 226. Before him, Jauch (1938) had published a list of all citrus weeds found in Germany and Switzerland, counting 814 species or forms. This list also included natives which he considered introduced by traffic. Fiedler was now able to increase this list to 870. He compared the number of alien plants in different cities and found that they had relatively few in common, even when the total number was not especially different. Remarkable also were the number of unicates (only one specimen during the whole observation time) and the fluctuations in the number of species recorded in a single year. The highest number of species was 128 in 1937, the lowest was 49 in 1936. The volume of imports and packing material did not change greatly so the explanation of these variations was due to weather conditions and the extent of weed killing.

Altogether 513 "hay-find" species were isolated in the course of 11 years in Leipzig from different packing materials. The total number of "hay-finds" observed in Germany was 692.

With Jauch (1938) the exploration of the citrus-weed flora in Germany came to its conclusion.[7] Besides his own observations and conclusions, Jauch gave a short survey of the historical development of the research on the citrus weed flora. He began with the astonishing statement that in the state herbarium of Baden there was not a single railroad plant from its capital of Karlsruhe. However, the Rhenish inland harbor of Karlsruhe had been systematically investigated for decades and 13 alien *Trifolium* species alone had been discovered. He repeated many conclusions which previous investigators had made. To Scheuermann's seven groups characterizing the kinds of introductions, Jauch added an eighth, segetal plants, plants introduced with seed material. He recognized that this phenomenon and its significance for agriculture was already well known to Zimmerman (1907).

The principal site of his research was the freight depot of the Karlsruhe main station which was an ideal place for the study of the citrus weeds. The station was a dead-end station situated in the inner city and no wool, cotton, cereals, or oil fruits were unloaded. Therefore, the percentage of the Mediterranean plants was especially high—93%, including some secondary introductions. It was higher than in any other German city. Altogether, in Karlsruhe 230 Mediterranean, 4 East European, 9 American, and 4 species of unclear origin were found during the five years from 1933 to 1937. He also compiled a list containing the names of all 814 citrus weeds found alive in Germany and Switzerland. Jauch was also able to determine when the railroads first began to bring citrus weeds to Germany.

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[7] However, Fiedler (1944b) and Müller (1950) later published supplements to their papers.

The first cars with southern fruits arrived in Freiburg, Baden, in 1895 and the first refuse dumping might have occurred in 1900.

Merxmüller (1952) described the altered conditions in the large München-Süd freight yard after World War II. He presumed that due to the cessation of southern fruit imports to Germany the adventive flora of the yards would have been wiped out. While citrus weeds primarily appeared around the unloading sites in the freight yards, the other introduced groups favored the places where the goods to which their seeds were attached were processed. Contrary to Merxmüller's expectation a noteworthy number of aliens were collected during several visits to the yard in 1948. Although many plants were of Mediterranean origin, they were not citrus weeds. His list was also in almost total disagreement with those previously published, and the same plants appeared increasingly on plant lists of neighboring countries. These new finds raised the question of recent migrations. Scheuermann's idea that many adventives found on railroads were not introduced by railroad traffic, but arrived there by active migration, found solid support. Of course, this strange accumulation of migrant plants was supplemented by introductions from freight and passenger trains and by sporadic true adventives.

Pedersen (1955) analyzed the origin of introduced plants found on the Danish railroads. Part of the plants were sown with impure seeds of alien origin. As is usually the case, the flora of the Danish stations was richer than that along the trunk lines. He concluded that the plants might have been introduced from surrounding localities, goods transfer, ballast, or the train itself. An important observation was made: "It may be accepted that the seed in the air circulation around a fast-moving train can be thrown up on the undercarriage where it can sit in crevices or in lubricating substances until they drop off at stations on account of vibration." Pedersen was also of the opinion that many railroad plants are "railway-wandering plants" which spread by active migration. He described this phenomenon for seven species.

Almquist (1957) gave a review of the botanical work done during the last hundred years in connection with the centennial jubilee of the Swedish railroads. He mentioned, among other things, several old reports of aliens found on embankments, but it was the same story as with the early German botanists: only the localities were stressed. The oldest reports (1859) were from the horse-drawn railroad.

Kornás et al. (1959) published their findings on the Polish railroads. In 1956 they quite thoroughly investigated the three most important freight yards in Krakow, as well as along the trunk lines for 12–16 km. Various statements made by them corresponded with those of other countries. The vegetation on the railroads was more or less xerophytic. Mesophytic vegetation was concentrated in overshadowed localities in the proximity of buildings and walls. Due to weed killing, annuals and biennials frequently only vegetated. Almost 400 species were recorded: 60.6% natives (apophytes) and 39.4% introduced (anthropophytes). Among the last, almost half were made up of archaeophytes. The percentage of the anthropophytes in the freight yards varied in accordance with the volume of the freight traffic in them.

Numerous Polish botanists published lists that frequently contained adventive novelties for the region. It was of interest to note that in quite a few cases after the publication of novelties, the same plants also began to appear in subsequent lists. Apparently after attention was called to these plants, many botanists began to go in search of them. This happened particularly with plants for which some kind of mimic was already known.

Among the hundreds of papers pertaining to railroad flora and vegetation, the one by Kreh (1960) is a treasure mine of information and is as important as the one by Matthies (1925). According to Kreh freight yards with aliens have always strongly attracted botanists. Therefore the vegetation of these yards has been well known floristically; but phytosociologists have paid little attention, and this is the approach he took. Over an observation period of 20 years in Stuttgart, he made very detailed observations on the influences of such factors as weed killers, manner of construction, construction material, soil, radiation, moisture, relief, operational techniques, manner and means of introduction, and competition on railroad vegetation. Operational techniques, freight traffic, and regularly performed weed killing using mainly chemicals were seen as the most important influences on railroad vegetation.

Hugentobler (1961) published an extensive paper on the adventive plants of the Swiss cantons St. Gallen and Appenzell, including a report by Heinrich Seitter. As was his compatriot, Schnyder, Seitter was also a railroadman. The most important conclusions of Seitter were as follows. Adventives arrived as seeds which under certain conditions stuck to car floors, in fissures of boards, on beams, on the runners of the doors, on the air slide doors of grain outlets. They fell to the ground and germinated during the normal unloading of the goods, at a collision of the cars on the switching tracks, by shaking during the movement of the train, and by blowing wind and rain. Although many seeds were shaken off, blown away, and washed by rain during train travel, areas between stations were relatively poor in plants. The adventives encountered too much competition from native plants, which were well fitted for the embankments. Thus big yields of adventives were restricted to those places where they were exempted from the competition of the natives, where the management was striving to keep the ground free of plants, such as switching tracks, unloading and dead-end tracks, military ramps, car wash installations, and places where dust and rubbish were deposited. Larger numbers of adventives might be expected where imported or transit livestock were loaded, fed, and watered. The rarest species might arrive with goods from the most distant regions, but in the era of chemical weed killing, the rare species will become increasingly rarer.

Knapp (1961) has described eight associations on the roadsides and the railroad in Hessen in West Germany. Those habitats which did not exist before industrialization have provided the potential for the development of special associations with a highly anthropogenic character. Naturalized plants played a large role in such associations in contrast to natural associations such as forests where immigration occurs seldom. The method of Braun-Blanquet (1951) was used. According to Knapp, it is quite possible that in railroad associations, as well as those along roadsides, particular ecotypes may gradually develop, then morphologically differentiated

taxa, initially varieties, later subspecies and species. But the time elapsed since the creation of these habitats has been too short for the realization of those possibilities.

Kausch & Heil (1965) investigated the microclimate and the plant cover on both slopes of a railroad embankment on a section of the Darmstadt-Eberbach trunk line in Hessen which stretches almost precisely in an east-west direction. The very distinct climatological conditions on these ideal southern and northern slopes separated by only a few meters corresponded to two distinct vegetation types.

In 1968 Messenger published "A railway flora of Rutland," the smallest county in England, recording 372 species. Alien plants were scarce. Of special interest were his observations on closed and dismantled lines. The distinctive character of the railroad flora was quickly lost after railroad management practices, which maintain it, were abandoned.

Interestingly, a general survey, carried out over ten years, showed that survey areas containing railroad property averaged 50 species more than those without railroad property, showing them to be the richest from the botanical standpoint.

Suominen (1969a, 1969b) studied the plant cover of Finnish railroad embankments and railroad yards. He stressed that the use of the railroad for ecological studies has been neglected and that the interest of botanists has been mainly directed to "railway plants" which are largely rare aliens and often casuals. The studies were entirely phytosociological in character, therefore, rare plants and adventives were excluded from consideration. This paper is a gold mine of information for anyone who wants to do phytosociological work on the railroad, but for the botanist who directs his interest mainly to "railway plants," this paper is of secondary importance.

Suominen noted that the historically more collected and noted, but rare and largely casual, aliens of railroad yards are poorly represented in the total vegetation. Their role in the vegetation is clearly subordinate. Suominen objected to my statement "ein ewig Kommen und ein ewig Gehen" (a perpetual coming and a perpetual going) (Mühlenbach, 1933:99) which characterized the course of things along the railroad in Riga. Suominen wrote ". . . while true of a considerable part of the species recorded from the yards, the description does not apply to any large proportion of the vegetation." On the other hand, Meyer (1932a), who has contributed so much to our knowledge of railroad vegetation, wrote once that "the greatest value has to be placed on these adventive plants when investigating the vegetation of railroad stations." These views, of course, succinctly reflect the different aims and work of phytosociologically and floristically oriented botanists.

Concomitantly with his compatriot Suominen, Niemi (1969a) published a related paper about railroad vegetation along an approximately 51 km section of the trunk line between Esbo and Ingå station in south Finland. During excursions in 1960, 1962, and 1963, records were made of the different plants and their distribution along the line and in 1965 special attention was paid to the different habitats afforded by the railroad and the various plant communities which they harbored. His investigations have shown that various habitats could

be distinguished depending upon which part of the embankment proper was scrutinized.

Gutte (1972), in the published version of his doctoral thesis, investigated the ruderal associations in western and central Saxony, as well as in some adjacent territories. He included the railroad in the scope of his work. The paper was based on 2,046 phytosociological records made on the basis of the Braun-Blanquet (1951) system. Among 38 established associations, 5 were found to occur on railroads. This was one more than Knapp (1961) had published, but the extra association was a special and limited one developing on the cinders from steam locomotives.

While a vast majority of botanists visiting the railroads, especially their freight yards, were engaged primarily in the hunt for introduced plants, a minority chose the study of associations as they develop on the railroads. There is a third group of botanists who published different classifications or systems based on ways of introduction. In each flora of a state or county or freight yard, attempts were made to distinguish between native plants and plants brought in through human activities. However, almost no one has restricted himself to an analysis of railroad adventives alone, but all have included other plants.

Watson (1847), in his *Cybele Britannica*, made the first attempt to publish a classification of plants according to their geographical origin, distinguishing five categories: 1. Native: apparently aboriginal species. 2. Denizen: at present maintaining its habitat as if a native, without the aid of man, yet liable to some suspicion of having been originally introduced. 3. Colonists: a weed of cultivated land or about houses and seldom found except in places where conditions have been favorably altered for its growth by man. 4. Alien: now more or less established, but either presumed or certainly known to have been originally introduced. 5. Incognita: reported as British, but requiring confirmation as such.

Curiously enough, "casuals" are mentioned in later literature as Watson's fourth group, but he did not use this term himself. De Candolle (1855) published his system in his botanical geography. He divided all plants into two groups, the cultivated and the spontaneously growing, the latter further subdivided as: 1. Adventives: of alien origin and badly established; may disappear. 2. Naturalized: well established in a country but positively of alien origin. 3. Probably of alien origin and 4. Perhaps of alien origin. Both 3 and 4 are well established, but the possibility of the alien origin is not certain; the doubts are stronger in the third than in the fourth category. 5. Natives: all species without any doubt as to origin; they must have existed in an epoch prior to human influence.

Ascherson (1883) used the Watson system, translating the terms into German. In 1887 Klinge used Greek to create an appropriate term. After a very brief discussion about the composition of the Baltic postglacial flora, he noted that man has been busy directly and indirectly altering the original physiognomy of the flora. By introducing a multitude of cultivated plants which frequently escape, and by spreading innumerable weeds, legitimate members of a flora appear. He termed this component a synanthropic flora. It differs from native floristic elements in that it does not have a geological history. Later this term was frequently used, sometimes in a deviating sense, possibly bringing some discredit to it. Now

it has more or less disappeared in German literature, but it is still very popular with Polish and Czechoslovakian botanists. I believe that it would be worthwhile to try to revitalize the term synanthrope which refers to a plant that has arrived with the help of man. The term was first used by Klinge. The later newly created terms were no better and were not needed.

Rikli (1903) introduced the term anthropochores, denoting with it those plants which settle without any assistance of man only in artificial habitats. Consequently, anthropochores include the entire ruderal and adventive flora. He distinguished several subgroups. One of these included the European segetal field weeds. Field weeds must have accompanied different cultivars which were introduced step by step by man in prehistoric times when the nomadic tribes began to settle and turn to agriculture. There is no doubt that the majority of weeds of neolithic grain fields came with the seed grain from the Near East, which is thought to be the home of the oldest cultivars in Europe. Doubt still exists for only a few weeds whether or not they were indigenous elements. As these weeds appeared in Europe thousands of years ago, European botanists have not considered them to be aliens. Rikli created the term archaeophytes for this very distinct group. They also came to America in the same way, but American botanists consider them as aliens and characterize them as introduced or naturalized from Europe. They have grown on American soil only a few hundred years and therefore their status is clearly different than in Europe. Another subgroup, the apophytes, should be mentioned. Apophytes are plants native in a region and normally growing in natural habitats, but showing a tendency to spread to artificial ones.

A very detailed classification system of the ruderal and adventive flora of the Swiss canton Zürich has been published by Naegeli & Thellung (1905). Although a joint publication, Thellung developed the classification so the system is widely known under his name. Thellung perfected his system in subsequent papers (1907, 1911–1912, 1915, 1918–1919, 1919) introducing some insignificant changes. A description of this system will be given after a short review of other authors who have created terminology for alien plants.

Simmons (1910) chose the general term hemerophytes based on the kind of habitats where alien plants alighted. Alien plants found on railroads could be attributed partly to his kenapophytes and partly to his chomapophytes. According to Linkola (1916) the term hemerophiles is preferable. Sterner (1938) returned to Klinge's term, synanthropes, but in his definition they are species whose immigration seems to involve human activity. To them belong not only escapes from culture and those species which were introduced unintentionally by man, but also those whose spontaneous immigration is made possible by the creation of suitable habitats through human activity. Walter (1954) used the term adventives, including under this cultivars. Jalas (1955) criticized the seemingly endless proliferation of technical terms for essentially the same phenomena, but developed his own classification on a character or feature of the habitats; chiefly how they were changed by man. Alien railroad plants found their place among his euhemerobes. He restricted the term anthropochory to cases when man personally performed the transfer. For all other events he proposed the term

hemerochory where the indirect activities of man in one or another form is the agent for transfer.

A system elaborated by Kreh (1957) presents difficulties in finding equivalent English or classical language terms for the German terms that he employed. They frequently differ in such slight nuances, that they could almost be considered as synonyms. Kreh complained that confusion has frequently prevailed in adventive botany by use of previously proposed terms for different concepts. His own system was later subjected to criticism and "improved" (Schroeder, 1968–1969). Kreh divided the plants of a flora into natives and foreigners. Foreigners were indoor and greenhouse plants, as well as "inconstant guests" (without any more explanation). Natives comprised wild plants and cultivated plants. Cultivated plants were subdivided into useful and ornamental plants. Wild plants were subdivided into original and adventive plants. Kreh emphasized that it was necessary to approach the problem of nomenclature of adventive plants from three different points of view. One must take into consideration the time of immigration, the degree of naturalization achieved, and the manner of immigration. For each approach he created special or unrelated terms. He also recognized a group of alien plants called "fraudulent or smuggled"[8] plants, overlooked by almost all previous writers. These plants have been sown or planted deliberately in natural habitats by such persons as bee keepers, collectors of medical herbs, lovers of aquaria, and idealistic botanophiles.[9] Of course, only a few would naturalize.

For the basis of his classification Kamyšev (1959) took into consideration the degree of adaptability, as well as the presumed genesis connected with the development of agriculture. There were difficulties including alien railroad plants in his scheme. They could be placed under his komophytes and partly under agriophytes, which should not be confused with his agrophytes.

The question of terminology came into discussion during the preparation for the *Flora Europaea*. Hylander (1961) recommended the use of "natives" and "aliens" in Scandinavian floras; the last being composed of "naturalized" and "casuals." Native and naturalized plants then comprise the "constant member of the wild flora."

The system of Holub & Jirásek (1967) is very extensive, employing 29 different

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[8] Kreh introduced the German expression *Angesalbte*. This word and the corresponding substantive *Ansalbung* found approval and appears now and then in German papers. The verb *ansalben* from which the words are derived has different meanings. In this case it apparently should mean "to cheat." Those plants are cheating the observer by leading him to believe that they are natives. I think that the word "fraudulent" would be an appropriate translation, but also "deceitful" or "deceptive" would not be incorrect expressions. Perhaps the second term "smuggled" plants (*eingeschmuggelt* in the original) might be best, at least in English. This term, created by Gradmann (1950), has been used by Kreh as a synonym. Müller-Schneider & Lhotská (1971) called deliberately introduced species ethelochores. Brenan and Eckardt (pers. comm.) suggest calling them imposturous plants.

[9] Brockmüller (1880) retold the story in his paper on plant migrations that Goethe constantly had with him the seeds of the sweet violet (*Viola odorata* L.) and that he disseminated them on his strolls around Weimar. Involuntarily one has to think about Johnny Appleseed who had the habit of scattering seeds in Ohio. Brockmüller thought that such premeditated falsification of nature is reprehensible. The practice has been prohibited since 1937 in Germany (Weber, 1961).

terms including those used previously by others and those contributed by themselves. In elaborating their classification, they paid attention to the influence of human activity, but also to the origin of the plants in the region, their adaptiveness to secondary habitats, their penetration into natural plant associations, and their degree of naturalization. For a railroad flora this detailed system is of little use because it demands knowledge of whether different plants observed on the railroad are able to establish themselves in natural habitats which are more or less free of human influence and how they behave there. On the railroad (at least in St. Louis) natural habitats are almost nonexistent.

Schroeder (1969) analyzed existing systems of terminology and found them mostly unsatisfactory. He pointed out that there have been attempts to combine three different principles on the basis of which plants could be classified: the time of their immigration, the manner of their immigration, and the degree of naturalization. He observed that the effort to create a universal system which takes into account all possibilities may in the end produce an unserviceable collection of words. For this reason, he proposed three independent systems. First, he considered the degree of naturalization and distinguished five categories: idiochorophytes (identical with the concept of natives), plants with a constant position in the primary natural vegetation; agriophytes, plants with a constant position in the potential natural vegetation, but not in the primary one; epecophytes, plants with a constant position in the actual but not in the potential natural vegetation; ephemerophytes, plants with no constant position in the vegetation, but occasionally growing wild; ergasiophytes, plants growing only in cultivation. Secondly, he considered the time of immigration and distinguished three categories: idiochorophytes, plants having immigrated before the activity of man; archaeophytes, plants whose man-supported immigration happened in "prehistoric" times; and neophytes, plants whose immigration took place in historic time. The third classification was based on the manner in which man supported plant immigration and consists of four categories: idiochorophytes, plants which immigrated without any aid of man; acolutophytes, plants whose immigration was supported only by the anthropogenic changes of vegetation which offered suitable habitats to the species migrating otherwise by their own abilities; xenophytes, plants whose diaspores have been introduced accidentally by man; and ergasiophygophytes, plants which have been introduced intentionally as cultivated plants and then escaped.

Most of the cited writers on terminology usually pointed out the weaknesses in the classifications of their predecessors. Trying to do away with them, they elaborated new schemes which often became more complicated. The system of Schroeder is the most applicable, although one has to keep in mind that there are three independent classifications.

Walter & Straka (1970) returned unconditionally to the original system of Thellung in their text book on phytology. Thellung's classification has, in fact, been used continually during these controversies by many field-workers, such as Kornás et al. (1959) and Jehlík & Slavík (1968), for example. Thellung (Naegeli & Thellung, 1905) used the terms apophytes and anthropochores. Together they constitute his anthropophytes which he placed on a par with Klinge's synanthropes.

Thellung divides anthropochores into seven categories and the apophytes into two categories as follows:

I. Anthropochores. Plants brought in by man.

A. By intentional activity of man: foreign cultivars and their derivatives.

1. Ergasiophytes. They include practically all cultivated plants such as grains, fruits, vegetables, forage, fiber, oil, and medicinal plants, and numerous ornamentals. They do not originate locally, and they all more or less need the care and protection of man to thrive.

2. Ergasiolipophytes. These are usually descendants of cultivars that are able to maintain themselves after the cultivation by man has ceased. They are frequently perennial and woody ornamentals. They are frequently found around the ruins of medieval castles in Europe, supposedly having persisted there since the Middle Ages. Similarly, in the flora of Missouri, many species persist in abandoned farmyards, old cemeteries, etc.

3. Ergasiophygophytes. This category is much larger than the preceding one. It consists of ergasiophytes or cultivars which have escaped without the knowledge of man from the place of cultivation and have settled on artificial or natural habitats. Mostly they disappear quite rapidly. In new localities they miss the support of man, and without his aid they mostly are not equal in competition with native plants and perish. In some cases they are able to adjust to prevalent conditions, especially climatic ones, and are capable of surviving competition and may even begin to spread. In rare cases they may grow rampantly and drive out the native flora. The most infamous example in the United States is *Lonicera japonica* Thunb. of which *Gray's Manual of Botany* said: "a most pernicious and dangerous weed, overwhelming and strangling the native flora and most difficult to eradicate." In the case of ornamentals, ergasiophygophytes are frequently called garden escapes.

B. By involuntary intervention of man: foreign weeds.

4. Archaeophytes. These are field weeds inadvertently introduced in prehistoric times with crops.

5. Neophytes. They occur relatively frequently and permanently in natural habitats and are often associated with the native vegetation. They do not depend on the continued activity of man to survive.

6. Epecophytes. These are plants that appeared in modern times, are more or less numerous, but are restricted to artificial habitats. They are dependent upon man for their existence in that he maintains those habitats or is compelled to create them again.

7. Ephemerophytes. These are plants that appear only sporadically as transients, almost exclusively on artificial habitats. A large part of a railroad flora belongs here.

II. Apophytes. Plants originally wild on natural habitats, but later growing in artificial ones.

A. By intentional activity of man.

8. Ekiophytes. They are native cultivated plants, grown as ornamental or useful plants.

B. Spontaneously establishing in artificial habitats.

9. Spontaneous apophytes.

Thellung's scheme just outlined is abbreviated because a few subgroups having no relation to a railroad flora are omitted. Thellung returned several times to the problem of terminology. Some slight changes were made and he combined archaeophytes and epecophytes in 1915 because they were equivalent. He also emphasized the importance of establishing anthropochores' immigration and introduction. The most elaborate scheme is given in his last paper (1919):

A. Weeds of foreign cultivars (useful and ornamental plants) introduced with seed material or as cuttings.

B. Species introduced by way of commerce and traffic.

1. With foreign grain and oil seeds; weed floras of mills, granaries or grain elevators, malt factories or mills, breweries, oil mills, mustard factories, and so on.
2. With cotton or wool; floras of wool washing establishments, cotton mills, cloth factories, and so on.
3. With the ballast of ships; older adventive floras of many harbors.
4. By traffic conveyances in general, trans-Atlantic ships, inland navigation on rivers and canals, truck and railroad traffic, passage of nomadic tribes (gypsies), transports of cattle, movements of armed forces and materials in wars.

There is no doubt that it is extremely difficult for a railroad botanist to keep apart the causes of weed introductions as characterized by subgroups A and B. Only in exceptional cases is it possible to discover the origin and the purpose of an import which occurred a year before. The situation is quite different when one examines weeds in a field or an orchard planted with imported seed material. The number of publications dealing with introductions under such circumstances is great. Frequently astonishing yields of adventive weeds are revealed. In such research Thellung's subgroup A is completely justified.

Stratiobotany is a term coined by Thellung (1917) to deal with the effects of war on vegetation. He wrote the paper while the war still raged, but the first authentic reports had become known. Even much earlier, the famous case of the siege of Paris (the florula obsidionalis) in the 1870–1871 war may be cited. An abundant exotic vegetation of Mediterranean species developed in the vicinity of Paris during the Franco-Prussian war (Gaudefroy & Movillefarine, 1871). Others who have published on this are Bonte (1930), Davidsson (1967), Koegeler (1949), Kupffer (1922), Pfeiffer (1956–1957), Salisbury (1943), Schreier (1955),

and especially the Finnish botanists Erkamo (1944–1946), Heikkinen (1959), Luther (1948–1949), Mannerkorpi (1944–1945), and Niemi (1969b). It was especially in World War II that the railroads, and especially the freight yards, were affected as they were always important military targets. The term polemochores, meaning followers of war, was coined by Mannerkorpi (1944–1945) to denote those alien plants introduced primarily as a result of war-related activities. A special group of polemochores are hippochores—plants introduced during a war by use of horses and their forage. In the spread of polemochores and hippochores railroads played by far the decisive role.

Naturally the question arises whether some of the synanthropes collected by me in St. Louis are polemochores from World War II. No definite proof exists, but it is highly probable that at least some polemochores arrived in St. Louis with military transports. The idea is supported by Fell's (1962) discovery of a very curious accumulation of western plants in a small area within Camp Grant in Winnebago County, Illinois. Fell considered two possibilities. They could be relics of dying populations; or, on the other hand, this particular tract was an important station and trench warfare training center during the war. Numerous horses and mules were shipped here from west of the Mississippi River, as were hay and straw in bales for use as bedding and in making ramparts for trenches and effigies for bayonet practice. Taking the European knowledge of hippochores into consideration, there is no doubt that only Fell's second explanation is valid. Finally, it must be said that this review of literature about railroad botany is by no means complete. An almost boundless literature exists in Europe on this subject. Nevertheless, I believe that the cited papers and books include some of the most important literature and give a definite understanding of this branch of botany.

History of Railroad Plants in Missouri

From the scanty literature it is apparent that interest in railroad plants has not been especially high in St. Louis. It is true that Eggert (1891) predicted that "railroads will bring new immigrants from other regions . . . ," but he did not mention a single case, although his list did contain some plants whose introduction by railroads is conceivable. Duggar (1922, as anonymous) wrote about plant immigrants in the St. Louis local flora. He stressed several modes of distribution, one of them being the railroads. He separated native North American plants (33 species) and "exotic" plants (19 species—mostly originating in Europe), and tried to draw a line between transient (13) and permanently established (6) immigrants. Of these 19 species 15 were also found by me, but, at least in Duggar's time, 9 were found only outside St. Louis. His region included most of St. Louis county and even a strip of Illinois, thus following the boundaries of the local St. Louis flora as established by the Engelmann Botanical Club (1911). There are also frequent references to railroad plants in Steyermark's (1963) *Flora of Missouri.*

In the western part of Missouri, the railroad flora has drawn much more attention. Jackson County, which includes Kansas City, Missouri, is botanically well examined and much regard was paid to the railroads, although the very

TABLE 1. Railroad companies (and acronyms) of St. Louis whose right-of-ways were studied for synanthropes.

1. Burlington-Northern (formerly Chicago, Burlington and Quincy RR) (BN).
2. Chicago & Eastern Illinois RR (C&EI).
3. Chicago, Rock Island, St. Paul and Pacific Lines (Rock Island RR) (RI).
4. Illinois Terminal RR (ITC).
5. Manufacturers Railway (MRS).
6. Missouri-Kansas-Texas RR (MKT).
7. Missouri Pacific RR (MP).
8. Norfolk & Western Railway (formerly Wabash RR) (N&W).
9. St. Louis-San Francisco (Frisco) Railway (SL-SF).
10. Terminal Railroad Association of St. Louis (TRRA).

first beginning was not especially encouraging. Bush (1882), whom Steyermark (1963) calls one of the most active collectors in Missouri, had started exploration with the hope that the flora would be greatly enlarged by seeds sown along the railroad lines. But already in his first report Bush (1882) admitted that "in this, however, we are disappointed, for very few plants have been introduced by the means above mentioned." But things soon began to change. Several supplements followed. In 1902 Mackenzie, assisted by Bush, published a *Manual of the Flora of Jackson County*. This time they found that "the expectation [to find many foreign plants in such an important railroad center as Kansas City] is amply borne out." Into the 1950s the Jackson County botanical studies were unsurpassed in Missouri.

STUDY AREA

Although many botanists have included the history of the botanically investigated railroad centers in their studies, this will not be attempted in this paper. The history of railroads in the United States is bewildering, and the railroad companies which touched St. Louis at one or another time far exceed 100 (Hyde & Conrad, 1899; Economic Educational Council of Greater St. Louis, n.d., 1959). In the present study the right-of-ways and freight yards of the ten remaining railroad companies in St. Louis were actually studied for their adventive flora. These companies and their abbreviations are listed in Table 1 and located in Fig. 1. Besides these ten, the St. Louis Water Works Railway which connected the city's water works was studied up to 1960. Only a few plants of interest were found here. The line is now dismantled. The numerous industrial sidings or spurs which are not directly owned by the railroad companies were, for the purposes of this study, ascribed to the railroad with which the spurs are connected.

As previously mentioned, the St. Louis metropolitan area has a railroad network that is the second largest in the U.S. Therefore strict restraints became inevitable. The railroads in East St. Louis and some other adjacent municipalities of Illinois were excluded, although the bulk of the railroads of the metropolitan area is located east of the Mississippi River. St. Louis County was also excluded and only the area of the City of St. Louis was used in this project. But even so

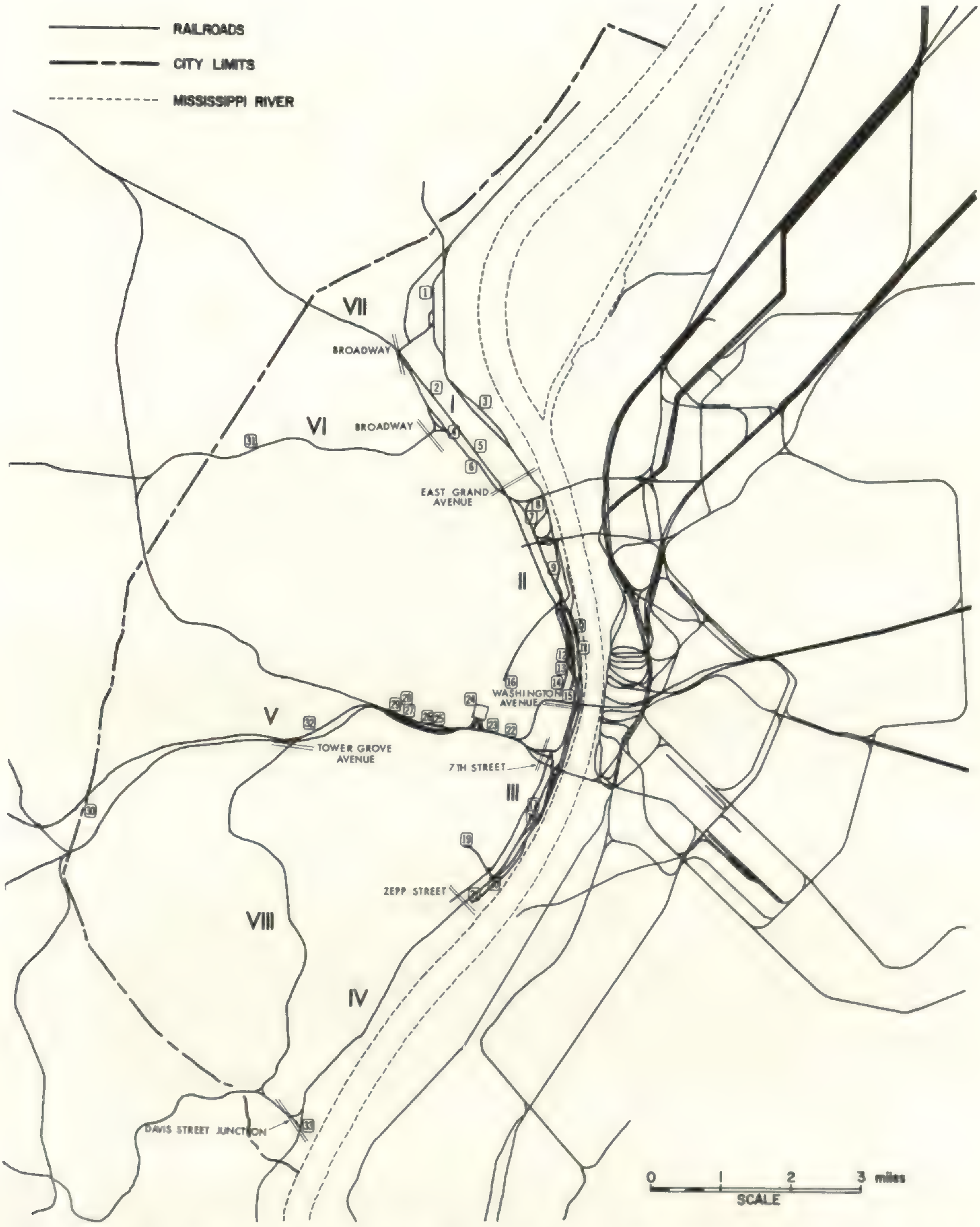

FIGURE 1. Railroad network in the city of St. Louis. See Table 2 for the names of the freight yards indicated by numbers in the figure. The double lines separate the regions.

the chosen area proved to be vast. It was not possible to get accurate information about the total length of all tracks in St. Louis, but it certainly extends many hundreds of miles. In order to increase the efficiency of collecting and to obtain a better idea of the distribution of the plants, the whole railroad network in the limits of the city of St. Louis was divided in eight regions (Fig. 1). The

first four regions are along the Mississippi River, along which most of the railroads settled, and the remaining four include the westward-pointed trunk or main lines.

Region 1. It stretches from the northern limit of the city to East Grand Ave. Freight yards 1–6 (Table 2) are located in it. The grain elevator of the St. Louis Grain Corporation is connected with the North St. Louis Freight Yard.

Region 2. It extends from East Grand Ave. to Washington Ave. and includes freight yards 7–16 (Table 2). Two grain elevators are located in the Tyler St. Yard (10). Here also runs the "High Line" tracks of ITC which for the most part are elevated, while the dead end is underground in downtown St. Louis.

Region 3. It stretches from Washington Ave. to Zepp St. The freight yards are 17–21 (Table 2). An elevator was located in the Lesperance St. Yard (17) but it burned down several years ago. Some tracks in this region are owned by the city of St. Louis, but are now leased and operated by the TRRA. Quite a few plants found on these city tracks are counted as TRRA plants.

Region 4. It extends from Zepp St. to the Davis St. Junction, which separates it from Region 8. It includes freight yard 33 (Table 2). Almost all tracks, as well as a big grain elevator, are owned by MP. A few short sidings of MRS laid on some streets and protruding south of Zepp St. are included in Region 4.

Region 5. It begins west of 7th St. but excludes the elevated tracks east of this street. The tracks run westward to Spring Ave., through the so-called Mill Creek Valley, for several miles, a section with the heaviest train traffic in St. Louis. Approximately 19 yards are located here, including 22–30 and 32 (Table 2) which were investigated. Numerous industrial spurs branch off in this region, and the grain elevator of the St. Louis Grain Corporation (Sarah Ave.) is located along the N&W line.

Region 6. The tracks (TRRA) branch off from the Harlem Freight Yard and Broadway is a boundary. Numerous industrial spurs branch from the main line and serve a multitude of industrial plants. Among them, the Pillsbury Company flour mills at Shreve Ave. are botanically important. The Pickrel Yard (31) (Table 2) is located in this region and an extensive net of spurs penetrates into the surroundings.

Region 7. This is the domain of N&W. It begins at the western end of the Luther Freight Yard at Broadway and is traversed by the trunk line to Omaha. In the city limits only two spurs branch off.

Region 8. This is the domain of MP. It begins west of the now dismantled Tower Grove Passenger Station (32) (Table 2) after a level crossing with the tracks of SF-SL (Tower Grove Avenue). The general course is at first to the west, but afterwards it turns south. From this trunk line to Little Rock, Ark., many spurs branch off, the longest being Christy Lead. Some railroads have a trackage right to use certain tracks of another company.

During the years of this study almost all tracks in the city were visited. The exceptions were the two tunnels and the existing elevated tracks of TRRA, ITC and MP, where vegetation could hardly be expected. Also no attempts were made to botanize the ascending grades to the four railroads carrying bridges.

TABLE 2. Freight yards in St. Louis studied for synanthropes.

1. Baden (MKT)
2. Luther (N&W)
3. North St. Louis (BN)
4. Harlem (TRRA)
5. Carrie Ave. (RI)
6. Bulver (TRRA)
7. Bremen (TRRA)
8. K Line (TRRA)
9. St. Louis Ave. (N&W)
10. Tyler St. (TRRA)
11. O'Fallon (TRRA)
12. Inbound Freight Yard (RI, SL-SF, C&EI)
13. Biddle Freight House (MP)
14. Wabash Fruit Terminal (N&W)
15. Carr St. (BN)
16. Freight Depot (ITC)
17. Lesperance St. (MP)
18. Lesperance St. (TRRA)
19. Miller St. (MRS)
20. River (MRS)
21. Cherokee (MRS)
22. 7th St. (SL-SF)
23. 18th St. (TRRA)
24. Union Station (TRRA)
25. East Jefferson (TRRA)
26. West Jefferson (TRRA)
27. South Ranken (TRRA)
28. Compton (TRRA)
29. North Ranken (TRRA)
30. Lindenwood (SL-SF)
31. Pickrel (TRRA)
32. Tower Grove Passenger Stations (closed) (MP, SL-SF)
33. Broadway Passenger Station (closed) (MP)

BACKGROUND TO THE STUDY

Altogether 563 excursions were carried out in 18 years (1954–1971), the minimum being 21 (in 1959) and the maximum 55 (1970) per year. The first years were spent becoming acquainted with the entire railroad network. Synanthropes can grow anywhere on the railroad, but are frequently found in great abundance in small areas. These rich places must be searched for since they are only distinguished by their richness in synanthropes. As a general rule, however, freight yards are richer in synanthropes than trunk or main lines. This is shown in that of the 208 St. Louis railroad species rated as very rare, 116 were found only in freight yards, 50 only along the trunk lines, and 42 in both places. Therefore more attention was normally paid to freight yards in the later years of this study, without neglecting trunk lines. A few of the most profitable places for finding synanthropes may be mentioned. Switching or classification tracks in the yards were rich in synanthropes during the early years. The bumping of cars during the classification operations often cause seeds, which become lodged on the cars in transit or in loading areas, to fall off, and clouds of dust can also be frequently seen. We have known since the time of Zimmermann (1907) that such dust may contain diaspores. Holding or storage yards and the buffers at the end of sidings were also good collecting places, but the richest areas were the so-called cleanout tracks, Carrie Ave. Yard (5) (RI), North St. Louis (3) (BN), Baden (1) (MRT) (see Table 2), where cars were cleaned before reloading. Refuse heaps accumulate along such tracks and many synanthropes may be found near them. In the St. Louis Ave. Freight Yard (9) (N&W) a certain track was also very rich in synanthropes. The reason for it was not easily discernible. Although I earlier expressed the idea that introductions might in this instance have been made from trucks from an adjoining parking lot (Mühlenbach, 1960), I have not been able to confirm this.

The introduction of the piggy-back method for freight movement during the

last 15 years initially seemed to result in a larger number of introductions, but also in an almost concomitant increase in the use of weed killers that quickly and effectively limited new introductions.

The surroundings of St. Louis grain elevators, in contrast to Europe, have not developed rich adventive floras. One reason is that in Europe imported grain from far away is often stored, while in St. Louis the elevators receive the grain primarily from Missouri and nearby states. But more important than the distance factor is the treatment of shipped grain. In St. Louis grain has already been cleaned, and this may well explain the poverty in synanthropes in the vicinity of grain elevators. The German elevators, for example, at least in earlier years, had to clean the Russian and Hungarian grain. The separated refuse was a rich source for synanthropes.

Likewise the visits to the St. Louis Produce Market, located on the St. Louis Ave. Freight Yard (N&W) and through which a huge amount of fruits and vegetables passes, were disappointing. Since most of the area is paved, one may only find potatoes, tomatoes, dill, lima beans, coriander, and some members of the gourd family growing in remote places, but practically no rare weeds and nothing similar to the rich citrus-weed flora found in Germany around similar establishments.

Hay or straw has never been observed to have been used as packing material. Poor results were achieved by visiting the St. Louis Terminals Corporation's harbor (North Market St.) or the courtyards and the receiving platforms, pens and cattle yards of Mayrose Packing Company's slaughterhouse (Vandeventer Ave.). Much better was the vicinity of Pillsbury Company flour mills, Shreve Ave. along the TRRA tracks, as well as in the courtyard of the mills. The surroundings of the Wabash Fruit Terminal (200 Carr St.) where fruit and vegetable shipments arrived were also good. Late in 1962 the use of this terminal for such purposes was discontinued and the synanthropic flora grew poor afterwards.

Yard margins frequently have a luxurious growth of plants in comparison with the tracks. This is in part due to the fact that weed-killing procedures are often not extended to the margins. However, the composition of the vegetation is much poorer along the margins but some species prefer these margins, as for example some composites and *Saponaria officinalis*, which is a rarity on the tracks but locally frequent just on the margins.

In some yards large unused lots were luxuriously overgrown with a tall vegetation that was for the most part much richer in species than that found on the margins. Synanthropes were not rare, but they were often ergasiophygophytes due to illegal dumping.

Synanthropes along trunk lines seemed to be most abundant along the MP line to the west (along Manchester Ave.) in Region 5 and along the N&W trunk line (along Gladys Ave.) in Region 7. A new kind of plant introduction, not mentioned in the cited literature, was discovered here. The percentage of ergasiophygophytes was unusually high. Heaps of hay were scattered about. It seemed that the owners of the nearby houses dumped their lawn cuttings on the railroad right-of-way. Plants obviously intentionally planted along the railroads were,

of course, not included in the list, but those growing on railroad property as a result of dumping of garden refuse were included. The industrial spurs or sidings contributed very little in general.

Only very slowly did I begin to realize that an important difference exists between the American and European railroad systems. One of the crucial differences is that in America most freight is delivered directly to industries without having to pass through a central freight house as in Europe. The majority of the St. Louis freight yards are simply classification yards that direct freight to industrial receiving points. Therefore, the opportunity for hitchhiking diaspores to escape on the railroads is much less than in Europe, where the bulk of goods is handled in the freight yards.

One of the factors that influences the dispersion of synanthropes currently is the trend to replace the uppermost layer of the ballast on which the tracks are laid, and for which grit or even sand has been traditionally used, with coarse crushed stones or gravel. This was done during the remodelling of the Luther Yard. It is clear that the old kind of surface allows germination and growth of plants much more readily than the modern gravel or crushed stones. Such remodeled tracks are often desolate throughout. If similar modernization of other freight yards should also be undertaken, it will be a formidable blow to the synanthropic flora of the yards, which is already for the most part under the scourge of weed-killing procedures.

I made every effort to pinpoint the exact localities of at least the rarer synanthropes. This was important so that their persistence following introduction could be determined. It was also important from another point of view. Many plants when discovered were frequently too young for certain determination. In the case of unicates these were left to mature and then collected later. In case of duplicated plants, some were taken and the rest were left to mature. Early on in this study it became clear that this was the best procedure since immature unicates could rarely be identified precisely, even by experts. In the case of larger unicate specimens, branches were collected at various stages of growth until adequate material for determination was obtained.

There are very frequent changes on the railroads. Tracks can be relocated, buildings demolished, whole yards abandoned and dismantled, businesses shut down or changed in ownership. During this long-term study, it was impossible to update the labels of the herbarium specimens to reflect these changes and all names on the labels reflect the names and conditions existing at the time of collection.

As previously mentioned, the prehistoric segetal weeds—archaeophytes—are considered to be introductions in America, in opposition to the prevailing European concept. Quite naturally these are included in the general list and treated like the later arrivals. Many of the archaeophytes have been naturalized in America, as happened earlier in Europe. It is clear that most of them grew here long before the railroad era began. Frankton & Mulligan (1974) reported that *Linaria vulgaris* was a serious weed in North America already in 1758, while *Capsella bursa-pastoris* was known before 1700. Surely quite a few of them came to the New World with the grain brought by the first immigrants. However,

indications of their early presence in Missouri can generally not be confirmed from herbarium records since the early collectors neglected weedy plants. For instance, of the 28 most common weeds of this study, only one sheet of *Sonchus oleraceus* (by Engelmann in 1839) was collected before 1851 (when the first railroad opened for traffic) based on the collections at the Missouri Botanical Garden.

Deliberately cultivated plants (ergasiophytes) were not taken into account in this study, but cultivated plants that naturally escape from cultivation (ergasiophygophytes) were recorded. A list of all the species (63) known to be cultivated as a useful plant in some part of the world was evaluated by Dr. A. E. Gaus (Cooperative Extension Service, Univ. of Missouri) as to their status of cultivation in Missouri. Some (such as *Abutilon theophrasti*, *Matricaria chamomilla*, and *Cichorium intybus*) have never been cultivated in Missouri (Gaus, pers. comm.). Many plants are cultivated only rarely. For example, *Secale cereale* is cultivated only "very little" and *Linum usitatissimum* was cultivated "30 years ago." Rye is now frequently encountered on the railroad, and flax is no rarity at all. Their seeds apparently come from far away. Of course, in most cases the origin of the ergasiophygophytes is quite clear—they are either escapes from gardens adjoining the railroad or their diaspores have been illegally dumped on the railroad premises. But sometimes such plants have been found in freight yards far away from gardens, amidst many weedy synanthropes that have come from far away. The possibility then cannot be denied that these ergasiophygophytes have been introduced without the direct help of man, and their status is the same as for noncultivated species introduced without direct help. In any case, ergasiophygophytes are included in my list, as so many European adventive botanists have done before me.

METHODS

It was clear from the beginning of this study that all plants encountered had to be collected since there was in most cases no way to decide whether they were native or synanthropic. The quantity of each collection depended upon the availability of the specimens and their sizes. Small plants were collected in large numbers, if they were numerous. With medium-sized plants 5–10 specimens were taken when there was no danger of exterminating the species. With very tall and weedy plants only parts were taken. Juvenile plants frequently presented difficulties. In such cases one or a few specimens were taken. Unicates mature enough for determination presented a problem. To remove them meant their demise. However, it was clear from the literature, as well as from my own experiences, that the majority of newly introduced synanthropes perish even if they are left undisturbed, and even if they have developed ripe fruits. Unicates were therefore "sacrificed" for the sake of the herbarium. Only juvenile unicates were left in the hope of collecting them later when more mature. From tall unicates, juvenile or mature, only parts were taken. It was not feasible to transplant juveniles (see Fiedler, 1944a). No attempt was ever made to propagate

plants artificially on the railroad, even when plenty of ripe seeds and fruits were available.

In 1954 each species encountered was collected for a total of 518 numbers, including, of course, some multiples. Beginning with 1955, a systematic compilation of all synanthropes was started with an estimation of their frequency. A list of known introductions in Missouri was compiled from Palmer & Steyermark's (1935) *Annotated Catalogue of the Flowering Plants in Missouri* and from Steyermark's (1963) *Flora of Missouri*, as well as from some other sources. In another list species were entered whose introduction could be anticipated. Many of these species were subsequently discovered, although a good number have not yet been found. They may not have been introduced, or they may have been missed for one reason or another. A more precise knowledge of distribution of the synanthropes was sought during the second half of this study. The general list of all hitherto discovered synanthropes and their distributions in each region was prepared and was amended when more synanthropes became known or when some previously included plant was disqualified. Of course, the recorded locations also increased vastly. These lists also showed considerable gaps in the distribution, many quite common plants missing in one or another region, and for the most common of these a deficiency index was prepared for each region. The corresponding indices were carefully scrutinized before each excursion. This helped immensely to fill in many of the gaps. Quite a few synanthropes were recorded in seven regions and there were no apparent reasons why they should not have grown in the eighth region, too. *Pastinaca sativa*, for example, is a frequently encountered plant, tall, conspicuous and gregarious, but it was never discovered in the quite large Region 4.

The occurrence of a plant can be examined from two points of view: how the plants are distributed over the entire railroad territory; and how they appear locally in the yards and on the right-of-ways. Eighty species were recorded in all eight regions. Their distribution is called "widespread." Twenty-eight plants were found in seven regions and are described as "quite widespread" plants. A widespread distribution does not indicate by any means that such a plant is numerous. Several are rarities (e.g., *Digitaria ischaemum*) and are seldom seen in many regions, sometimes even as unicates, although many of the widespread plants do indeed compose the dominant part of the railroad vegetation.

There have been many proposals to describe frequency of plants in a given area. The mathematical system advocated by Henker (1960), although precise, was not applicable in this study because of the very strong fluctuations in a railroad flora that is not growing in a natural habitat and because of the constant reintroductions of species. Other systems have been proposed by Braun-Blanquet (1951) and Nelson (1963), among others. However, for the purpose of this study it seemed best to use five categories of frequency: common, frequent, scattered, rare, and very rare. Each taxon was considered to be very rare if it was observed in not more than five localities during the 18 years of this study. Repeated observations of the same plant in the same place through the years were not counted. Plants were considered to be rare if they were observed in between 6 and 40 localities. The evaluation of the remaining categories was

entirely subjective and was subject to change throughout this study because of the very large fluctuations of many plants. In order to maintain the accuracy of this system I avoided excursions beyond the railroad in all the years of this study so that the categorizations of frequency is based entirely on the actual conditions along the railroad.

SYSTEMATIC SECTION

Table 3 lists the distribution of the synanthropes in the eight regions. Infraspecific taxa as far as available, are included. I decided not to list plants whose determination was not certain, although I was urged by several persons to do so. This could, I was told, encourage a search for them in the future, but I very much doubt that there will be followers of this kind of work in St. Louis. Also, my experiences in Riga have shown that little can be achieved by publishing uncertain plants. My predecessor in Riga, Rothert (1915), inserted into his list quite a few plants with question marks, but only a part of them was later found by me in my 20 years of work in Riga. Many of the doubtful species in St. Louis were hybrids.

In the following section each species is discussed in detail. The sequence of species follows Fernald's (1950) *Gray's Manual of Botany*. Fifty-five species are not mentioned in the *Manual*; they are included as seemed most appropriate. Previously unpublished Missouri taxa are printed in **boldface** type. Some species from Missouri based on old records were excluded from the *Flora of Missouri* by Steyermark (1963) as erroneously determined. Those now collected are treated as novelties and are also printed in **boldface** type. Species connected in the literature with my name, but which later proved to be something else are enclosed in [brackets]. The nomenclature often deviates from that of *Gray's Manual of Botany* and the *Flora of Missouri*. The names used were preferred by the specialists who determined the collections. In such cases the customarily used names are mentioned as synonyms. The same was done in other cases where it seemed appropriate. The naming of some cultigens presented difficulties. Anderson (1967) strongly opposed the use of such names as *Iris germanica* L. because of its unquestionably hybrid nature. Nevertheless, most floras use this name for this well-known ornamental and its escapes, so I decided to follow this practice.

For the largest group—the very rare plants (not more than 5 localities in 18 years)—the following information is given: my collecting number,[10] date(s), and the number of observed specimens. In case of taxa unpublished for Missouri the locality is given, as well as the name of the botanist who determined it. When a plant during these years was found in six or more localities, this information is not mentioned unless some extraordinary event seemed to merit some

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[10] Persons interested in exact localities may consult most of the relevant voucher specimens deposited at MO; a few specimens are deposited in other herbaria and the voucher information is followed by the acronym of that herbarium. For rare plants that were only observed, not collected, the full locality data is given in the text. Mühlenbach is abbreviated as *M*; different localities are separated by periods; collections from the same locality collected at different times are separated by semicolons.

TABLE 3. Distribution of synanthropes in the eight regions of St. Louis railroads (see also Table 1 and Fig. 1).

Taxa	Region I	II	III	IV	V	VI	VII	VIII
GRAMINEAE								
Bromus inermis Leyss.	+	+	+	+	+	+	+	+
B. unioloides Kunth	+	+						
B. secalinus L.	+		+	+	+	+		
B. japonicus Thunb. subsp. *japonicus*	+	+	+	+	+			+
subsp. *subsquarrosus* (Borb.) Pénzes	+	+		+	+	+		
B. commutatus Schrad.	+	+	+	+	+	+	+	+
B. squarrosus L.	+		+					
B. rigidus Roth		+						
B. tectorum L.	+	+	+	+	+	+	+	+
Festuca rubra L. var. *commutata* Gaudin	+		+					
F. pratensis Huds.	+		+		+	+		+
F. arundinacea Schreb.	+	+	+	+	+	+	+	+
F. myuros L.			+		+			
Puccinellia distans (L.) Parl.			+					
P. airoides (Nutt.) Wats. & Coult.	+							
Poa annua L.	+			+	+			
P. compressa L.	+	+	+	+	+	+	+	+
Dactylis glomerata L.	+	+	+	+	+	+	+	+
Eragrostis curtipedicellata Buckley					+			
E. oxylepis (Torr.) Torr.		+						
E. multicaulis Steud.						+		
E. cilianensis (All.) E. Mosher	+	+	+	+	+	+	+	+
E. minor Host	+	+	+	+	+	+	+	+
E. barrelieri Daveau		+						
E. elliottii S. Wats.		+						
E. curvula (Schrad.) Nees			+					
Cynosurus echinatus L.			+					
Agropyron desertorum (Fisch.) Schult.		+						
A. repens (L.) Beauv.	+	+	+	+	+	+	+	+
A. elongatum (Host) Beauv.			+					
Aegilops cylindrica Host	+	+	+	+	+	+	+	+
Lolium perenne L.	+		+		+			+
L. multiflorum Lam.	+	+	+	+	+	+	+	+
L. persicum Boiss. & Hohen.	+	+						
L. rigidum Gaudin			+					
Hordeum jubatum L. var. *caespitosum* (Scribn.) Hitchc.		+						
H. vulgare L.	+	+	+	+	+	+		+
Triticum aestivum L.	+	+	+	+	+	+	+	+
Secale cereale L.	+	+	+	+	+	+	+	+
Holcus lanatus L.			+					
Avena fatua L.	+	+	+	+	+	+	+	+
A. sativa L.	+	+	+	+	+	+	+	+
Aira elegans Willd.			+					
Apera spica-venti (L.) Beauv.	+	+	+	+	+			
A. interrupta (L.) Beauv.	+							
Crypsis schoenoides (L.) Lam.	+	+			+			
Phleum pratense L.	+	+	+	+	+	+	+	+
Cynodon dactylon (L.) Pers.	+	+	+	+	+	+	+	+
Chloris virgata Swartz	+							
Eleusine indica (L.) Gaertn.	+	+	+	+	+	+	+	+
Leptochloa dubia (H.B.K.) Nees			+					
Phalaris canariensis L.	+	+	+		+			

Table 3. (Continued)

Taxa	Region I	II	III	IV	V	VI	VII	VIII
GRAMINEAE (continued)								
Anthoxanthum odoratum L.	+							
Digitaria ischaemum (Schreb.) Schreb. ex Muhl.	+	+	+	+	+	+	+	+
D. sanguinalis (L.) Scop.	+	+	+	+	+	+	+	+
Eriochloa contracta Hitchc.	+							
Paspalum dilatatum Poir.		+						
P. urvillei Steud.	+	+						
Panicum geminatum Forsk.		+						
P. texanum Buckley	+							
P. miliaceum L.	+	+	+		+			
Echinochloa colonum (L.) Link	+	+	+					
E. crusgalli (L.) Beauv. f. *crusgalli*	+	+	+	+	+	+	+	+
f. *longiseta* (Trin.) Farw.	+	+	+	+	+	+	+	+
Setaria glauca (L.) Beauv.	+	+	+	+	+	+	+	+
S. *verticillata* (L.) Beauv. var. *verticillata*	+	+	+	+	+	+		+
var. *ambigua* (Guss.) Parl.			+	+				
S. *viridis* (L.) Beauv. var. *viridis*	+	+	+	+	+	+	+	+
var. *major* (Gaudin) Posp.		+						
S. *faberi* Herrm.	+	+	+	+	+	+	+	+
S. *italica* (L.) Beauv.	+		+					
Pennisetum ciliare (L.) Link		+						
Miscanthus sinensis Anderss.	+				+	+		+
Erianthus ravennae (L.) Beauv.	+							
Sorghum halepense (L.) Pers.	+	+	+	+	+	+	+	+
S. *bicolor* (L.) Moench	+	+	+	+	+	+		+
S. *dochna* (Forsk.) Snowden var. *technicum* (Koern.) Snowden	+	+						
Zea mays L.	+	+	+	+	+	+	+	+
CYPERACEAE								
Carex nebraskensis Dewey	+							
COMMELINACEAE								
Commelina communis L.	+	+	+	+	+	+	+	+
JUNCACEAE								
Juncus gerardii Loisel.					+			
LILIACEAE								
Allium sativum L.	+		+	+	+	+	+	+
A. vineale L. f. *vineale*	+	+	+	+	+	+	+	+
f. *compactum* (Thuill.) Aschers.	+	+						
A. cepa L. var. *cepa*		+						
var. *viviparum* Metz				+				
Hemerocallis fulva L. var. *fulva*	+	+	+	+	+	+	+	+
var. *kwanso* Regel	+			+				+
Ornithogalum umbellatum L.						+		+
Muscari botryoides (L.) Mill.							+	
Yucca filamentosa L.							+	
Asparagus officinalis L.	+	+		+	+	+	+	+
AMARYLLIDACEAE								
Narcissus × *biflorus* Curtis								+
IRIDACEAE								
Iris germanica L.	+						+	+

TABLE 3. (Continued)

Taxa	Region I	II	III	IV	V	VI	VII	VIII
ULMACEAE								
Ulmus pumila L.	+	+	+	+	+	+	+	+
MORACEAE								
Morus alba L.	+	+	+	+	+	+	+	+
Broussonetia papyrifera (L.) Vent.				+				
Maclura pomifera (Raf.) Schneid.	+	+		+	+	+		+
CANNABINACEAE								
Cannabis sativa L.		+		+	+			
Humulus japonicus Sieb. & Zucc.	+	+	+	+	+	+	+	+
POLYGONACEAE								
Rumex patientia L.	+	+	+	+	+	+	+	+
R. crispus L.	+	+	+	+	+	+	+	+
R. pulcher L.		+	+					
R. obtusifolius L.			+	+	+			+
R. stenophyllus Ledeb.	+	+		+	+			
R. dentatus L.	+							
R. acetosella L.	+	+	+	+	+	+	+	+
Polygonum pensylvanicum L. var. *rosaeflorum* J. B. S. Norton	+	+		+		+		
P. lapathifolium L. var. *prostratum* Wimm.			+					
P. scabrum Moench	+	+						
P. orientale L.					+			
P. cespitosum Blume var. *longisetum* (DeBruyn) Stewart	+		+		+		+	+
P. persicaria L. f. *persicaria*	+	+	+	+	+	+	+	+
f. *albiflora* Millsp.		+						
P. convolvulus L.	+	+	+	+	+	+	+	+
P. cuspidatum Sieb. & Zucc.	+	+	+	+	+	+		+
Fagopyrum sagittatum Gilib.	+	+	+		+		+	
CHENOPODIACEAE								
Kochia scoparia (L.) Schrad.	+	+	+	+	+	+	+	+
K. iranica (Hausskn. &. Bornm.) Litw.	+							
Chenopodium murale L.	+					+		
C. botrys L.	+	+	+	+	+	+		+
C. ambrosioides L.	+	+	+	+	+	+		+
C. pumilio R. Br.	+	+						
C. glaucum L. var. *glaucum*	+							
var. *salinum* (Standley) Boivin	+							
C. watsonii A. Nelson	+							
C. opulifolium Schrad.					+			
Atriplex rosea L.	+							
A. truncata (Torr.) Gray	+		+					
A. heterosperma Bunge						+		
Salsola kali L. var. *tenuifolia* Tausch	+	+	+		+	+		+
S. collina Pall.	+	+	+		+	+		
Beta vulgaris L.					+			
AMARANTHACEAE								
Celosia cristata L.	+			+			+	
Amaranthus palmeri S. Wats.	+	+	+	+	+			+
A. arenicola I. M. Johnston	+	+						
A. hybridus L.	+	+	+	+	+	+	+	+
A. retroflexus L.	+	+	+	+	+	+	+	+

TABLE 3. (Continued)

Taxa	Region I	II	III	IV	V	VI	VII	VIII
AMARANTHACEAE (continued)								
A. powellii S. Wats.	+	+	+			+		
A. spinosus L.	+	+	+		+			
A. tricolor L.							+	
AIZOACEAE								
Mollugo verticillata L.	+	+	+	+	+	+	+	+
PORTULACACEAE								
Portulaca oleracea L.	+	+	+	+	+	+	+	+
P. grandiflora Hook.	+	+	+	+			+	+
CARYOPHYLLACEAE								
Arenaria serpyllifolia L.	+	+		+	+	+		+
Stellaria media (L.) Cyrillo	+	+	+	+	+	+	+	+
Cerastium holosteoides Fries subsp. *triviale* (Link) Möschl f. *glandulosum* (Boenn.) Möschl	+	+			+		+	+
C. glomeratum Thuill.					+			
C. semidecandrum L.				+				
C. pumilum Curtis f. *pumilum*	+	+			+		+	
f. *medium* Möschl			+		+	+		+
Holosteum umbellatum L.	+			+				+
Agrostemma githago L.	+	+	+	+	+	+		+
Lychnis alba Mill.	+	+	+	+	+			
Silene cucubalus Wibel	+	+	+					
S. cserei Baumg.		+		+	+			
S. armeria L.							+	
S. conoidea L.	+	+	+					
S. dichotoma Ehrh.		+						
S. gallica L.	+							
S. noctiflora L.	+	+	+		+			
Saponaria officinalis L.	+	+	+	+	+	+	+	+
S. vaccaria L.	+	+	+		+	+		
Dianthus armeria L.	+	+			+	+		
RANUNCULACEAE								
Ranunculus acris L.					+			
R. sardous Crantz	+					+		
R. arvensis L.	+							
Clematis dioscoreifolia Lévl. & Vaniot	+				+		+	
Delphinium ajacis L.	+	+	+	+	+	+	+	+
D. consolida L.		+						
PAPAVERACEAE								
Eschscholtzia californica Cham.	+							
Argemone albiflora Hornem.	+	+						
CAPPARACEAE								
Cleome hassleriana Chod.	+							
CRUCIFERAE								
Berteroa incana (L.) DC.	+							
Lobularia maritima (L.) Desv.							+	
Thlaspi arvense L.	+	+	+	+	+	+	+	+
Lepidium perfoliatum L.	+	+	+	+				
L. campestre (L.) R. Br.	+	+	+	+	+	+		+
Cardaria draba (L.) Desv.				+	+			

TABLE 3. (Continued)

Taxa	Region							
	I	II	III	IV	V	VI	VII	VIII
CRUCIFERAE (continued)								
C. pubescens (C. A. Mey.) Rollins var. *elongata* Rollins	+	+	+					
Capsella bursa-pastoris (L.) Medic.	+	+	+	+	+	+	+	+
Camelina microcarpa Andrz.	+	+	+	+	+	+		
Neslia paniculata (L.) Desv.	+	+						
Raphanus raphanistrum L.	+	+	+		+	+		
R. sativus L.	+	+						
Brassica hirta Moench	+	+	+		+	+		+
B. kaber (DC.) L. C. Wheeler	+	+	+	+	+	+	+	+
B. juncea (L.) Coss. var. *juncea*	+	+	+	+	+			+
var. *crispifolia* Bailey	+	+	+					
B. nigra (L.) Koch	+		+		+			
B. rapa L.	+	+	+	+		+	+	
B. napus L. var. *napobrassica* (L.) Peterm.			+	+				
Erucastrum gallicum (Willd.) O. E. Schulz	+	+		+	+	+		
Conringia orientalis (L.) Dumort.	+	+	+	+	+			
Sisymbrium officinale (L.) Scop. var. *leiocarpum* DC.	+	+	+		+			
S. altissimum L.	+	+	+	+	+	+		+
S. loeselii L.	+	+	+					
Arabidopsis thaliana (L.) Heynh.	+	+			+			
Descurainia sophia (L.) Webb	+	+	+	+	+	+		
Erysimum repandum L.	+	+	+	+	+	+	+	+
Barbaraea vulgaris R. Br.	+		+	+	+	+		+
Chorispora tenella (Pall.) DC.	+	+	+		+	+		
CRASSULACEAE								
Sedum sarmentosum Bunge							+	+
SAXIFRAGACEAE								
Philadelphus coronarius L.								+
ROSACEAE								
Pyrus communis L.					+			
P. malus L.		+	+		+			+
P. baccata L.					+			
Fragaria × *ananassa* Duchesne					+			
Potentilla argentea L.			+					
P. recta L.	+	+	+	+	+	+		+
Rubus bifrons Vest								+
Rosa multiflora Thunb.		+	+	+	+	+	+	+
R. rugosa Thunb.								+
Prunus persica (L.) Batsch	+	+	+	+	+	+	+	+
P. armeniaca L.		+						
LEGUMINOSAE								
Cassia occidentalis L.	+							
Trifolium incarnatum L.					+			
T. pratense L. f. *pratense*	+	+	+	+	+	+	+	+
f. *leucochraceum* Aschers. & Prantl								+
T. repens L.	+	+	+	+	+	+	+	+
T. hybridum L.	+	+	+	+	+	+		+
T. campestre Schreb.			+		+			
T. dubium Sibth.					+		+	

TABLE 3. (Continued)

Taxa	Region I	II	III	IV	V	VI	VII	VIII
LEGUMINOSAE (continued)								
Melilotus officinalis (L.) Lam. f. *officinalis*	+	+	+	+	+	+	+	+
f. *confertus* O. E. Schulz				+				
M. albus Desr.	+	+	+	+	+	+	+	+
Medicago sativa L.	+	+	+		+	+	+	+
M. lupulina L. var. *lupulina*	+	+		+	+	+	+	+
var. *glandulosa* Neilr.	+	+	+	+	+	+	+	+
M. polymorpha L. var. *vulgaris*								
(Benth.) Shinners		+						
Coronilla varia L.					+			
Lespedeza cuneata (Dumont) G. Don			+		+			
L. striata (Thunb.) H. & A.					+			
L. stipulacea Maxim.	+	+	+	+	+	+		+
L. bicolor Turcz.					+			
Vicia sativa L. var. *nigra* L.	+							
V. cracca L.	+							
V. villosa Roth	+	+	+	+		+		
V. dasycarpa Ten.			+	+	+		+	
Lathyrus hirsutus L.		+			+			
L. latifolius L.	+			+	+		+	+
Pisum sativum L. var. *sativum*	+							
var. *arvense* (L.) Poir.						+		
Phaseolus vulgaris L. var. *humilis* Alef.	+							
P. lunatus L. var. *lunonanus* Bailey		+						
Glycine max (L.) Merr.	+	+	+	+	+	+	+	+
LINACEAE								
Linum usitatissimum L.	+	+	+		+	+		
OXALIDACEAE								
Oxalis priceae Small subsp. *texana* (Small) Eiten							+	
GERANIACEAE								
Erodium cicutarium (L.) L'Hér.	+							
E. texanum Gray	+							
ZYGOPHYLLACEAE								
Tribulus terrestris L.	+	+	+	+	+	+	+	+
SIMAROUBACEAE								
Ailanthus altissima (Mill.) Swingle	+	+	+	+	+	+	+	+
EUPHORBIACEAE								
Croton texensis (Klotzsch) Muell. Arg.	+							
C. lindheimerianus Scheele					+			
Ricinus communis L.	+	+			+			
Chamaesyce prostrata (Ait.) Small	+		+					
ANACARDIACEAE								
Rhus typhina L. f. *dissecta* Rehder					+			
CELASTRACEAE								
Euonymus fortunei (Turcz.) Hand.-Maz.								
var. *radicans* Rehder					+			
BALSAMINACEAE								
Impatiens balsamina L.							+	

TABLE 3. (Continued)

Taxa	Region							
	I	II	III	IV	V	VI	VII	VIII
VITACEAE								
Parthenocissus tricuspidata (Sieb. & Zucc.) Planch.					+			+
Vitis labruscana Bailey				+				
MALVACEAE								
Malva sylvestris L.							+	
M. neglecta Wallr.			+					
M. rotundifolia L.	+		+			+		
Alcea rosea L.	+	+	+	+	+	+	+	+
Anoda cristata (L.) Schlecht.			+					
Sida spinosa L.	+	+	+	+	+	+	+	+
Abutilon theophrasti Medic.	+	+	+	+	+	+	+	+
Hibiscus syriacus L.				+	+			
H. trionum L.	+	+	+					
Gossypium hirsutum L.	+	+						
STERCULIACEAE								
Melochia corchorifolia L.		+						
GUTTIFERAE								
Hypericum perforatum L.	+			+	+			+
TAMARICACEAE								
Tamarix gallica L.					+			
VIOLACEAE								
Viola tricolor L.								+
V. kitaibeliana R. & S. var. *rafinesquii* (Greene) Fern.	+	+		+	+	+	+	+
ONAGRACEAE								
Oenothera kunthiana (Spach) Munz		+						
Gaura sinuata Nutt. ex Ser.	+							
ARALIACEAE								
Hedera helix L.					+			
UMBELLIFERAE								
Anthriscus scandicina (Weber) Mansf.			+					
Torilis arvensis (Huds.) Link	+	+	+	+	+	+	+	+
T. nodosa (L.) Gaertn.		+						
Coriandrum sativum L.		+						
Conium maculatum L.	+	+		+				+
Apium graveolens L.		+						
Ammi majus L.		+						
Anethum graveolens L.		+						
Pastinaca sativa L.	+	+	+		+	+	+	+
Daucus carota L.	+	+	+	+	+	+	+	+
PRIMULACEAE								
Anagallis arvensis L.	+	+	+		+			
LOGANIACEAE								
Buddleia davidii Franch.					+			
ASCLEPIADACEAE								
Asclepias subverticillata (Gray) Vail		+						

TABLE 3. (Continued)

Taxa	Region I	II	III	IV	V	VI	VII	VIII
CONVOLVULACEAE								
Ipomoea coccinea L.		+		+	+			+
I. hederacea (L.) Jacq. var. *hederacea*	+	+	+	+	+	+	+	+
var. *integriuscula* Gray	+	+	+	+				
I. purpurea (L.) Roth var. *purpurea*	+	+	+	+	+	+	+	+
var. *diversifolia* (Lindl.) O'Donell								+
I. cairica (L.) House	+							
Jacquemontia tamnifolia (L.) Griseb.		+	+					
Convolvulus pellitus Ledeb. f. *anestius* Fern.	+				+			
C. arvensis L.	+	+	+	+	+	+	+	+
Cuscuta indecora Choisy var. *neuropetala* (Engelm.) Hitchc.		+						
BORAGINACEAE								
Heliotropium indicum L.	+							
Echium vulgare L.	+							
Lithospermum arvense L.	+	+	+	+	+	+	+	+
Amsinckia lycopsoides Lehm.	+	+	+					
A. hispida (R. & P.) Johnston	+							
A. tesselata Gray	+			+				
Lappula echinata Gilib.	+	+			+	+		
L. redowskii (Hornem.) Greene var. *redowskii*	+							
VERBENACEAE								
Verbena brasiliensis Vell.				+				
V. halei Small	+	+						
LABIATAE								
Nepeta cataria L.	+	+	+		+			
Glechoma hederacea L. var. *micrantha* Moricand			+			+	+	+
Dracocephalum parviflorum Nutt.	+		+					
Leonurus cardiaca L.	+	+		+	+	+	+	+
Galeopsis tetrahit L.	+	+				+		
Lamium amplexicaule L. f. *amplexicaule*	+	+	+	+	+	+	+	+
f. *clandestinum* (Reichenb.) G. Beck	+	+		+	+	+	+	+
L. purpureum L.				+	+		+	+
Mentha spicata L.			+					
M. × *gentilis* L.	+	+		+				+
Perilla frutescens (L.) Britt.	+	+			+	+		
Ocimum basilicum L.	+							
SOLANACEAE								
Solanum tuberosum L.	+	+	+					
S. sarachoides Sendtner		+						
S. rostratum Dunal	+	+	+	+	+			+
Lycopersicum esculentum Mill.	+	+	+	+	+	+	+	
Physalis viscosa L. var. *cinerascens* (Dunal) Waterfall	+							
P. acutifolia (Miers) Sandw.	+							
Lycium halimifolium Mill.	+	+	+	+	+	+	+	+
Datura stramonium L. var. *stramonium*	+	+	+	+	+	+		+
var. *tatula* (L.) Torr.	+							
D. innoxia Mill.	+		+		+		+	
Petunia axillaris (Lam.) B. S. P.	+							
P. × *atkinsiana* D. Don	+			+	+			+

TABLE 3. (Continued)

Taxa	Region I	II	III	IV	V	VI	VII	VIII
SCROPHULARIACEAE								
Verbascum thapsus L.	+	+	+	+	+	+	+	+
V. blattaria L. f. *blattaria*	+	+	+	+	+	+		+
f. *erubescens* Brugger	+	+	+	+	+	+		+
Kickxia elatine (L.) Dumort.	+		+	+	+			+
Linaria vulgaris Hill	+	+					+	+
Antirrhinum majus L.	+							
Chaenorrhinum minus (L.) Lange	+	+			+	+		
Paulownia tomentosa (Thunb.) Steud.								+
Veronica arvensis L.	+	+	+	+	+	+	+	+
V. polita Fries							+	
BIGNONIACEAE								
Catalpa bignonioides Walt.					+			
PEDALIACEAE								
Sesamum orientale L.		+						
PLANTAGINACEAE								
Plantago major L.		+	+		+			+
P. lanceolata L.	+	+	+	+	+	+	+	+
P. wrightiana Dcne.	+				+			
CAPRIFOLIACEAE								
Lonicera xylosteum L.					+			
L. morrowii Gray								+
L. japonica Thunb.	+		+	+	+	+	+	+
DIPSACACEAE								
Dipsacus sylvestris Huds.	+					+		
CUCURBITACEAE								
Cucurbita pepo L. var. *ovifera* (L.) Alef.	+		+					
Cucumis melo L.	+	+	+					
C. sativus L.	+							
Citrullus lanatus (Thunb.) Mansf.	+	+	+	+	+	+	+	
Lagenaria siceraria (Molina) Standley					+		+	+
CAMPANULACEAE								
Campanula rapunculoides L.							+	
COMPOSITAE								
Eupatorium capillifolium (Lam.) Small	+				+			
Grindelia squarrosa (Pursh) Dunal var. *serrulata* (Rydb.) Steyerm.	+							
Gutierrezia texana (DC.) T. & G.	+							
Franseria discolor Nutt.	+							
Ratibida tagetes (James) Barnhart	+							
Verbesina encelioides (Cav.) B. & H. var. *exauriculata* Robins. & Greenm.	+	+	+		+			
Coreopsis cardaminefolia (DC.) T. & G.	+							
Bidens coronata (L.) Britt.	+							
B. pilosa L. var. *radiata* Schz.-Bip.	+							
Cosmos bipinnatus Cav.	+							
C. parviflorus (Jacq.) Pers.	+							
Galinsoga ciliata (Raf.) Blake	+	+						
Gaillardia pulchella Foug.	+						+	
Tagetes patula L.	+				+			

Table 3. (Continued)

Taxa	Region I	II	III	IV	V	VI	VII	VIII
COMPOSITAE (continued)								
Achillea millefolium L.	+	+	+	+	+	+	+	+
Anthemis cotula L.	+	+	+		+	+		
A. arvensis L.	+	+		+				
Matricaria chamomilla L.	+		+	+	+			
M. matricarioides (Less.) Porter	+	+	+					
Chrysanthemum leucanthemum L.	+	+	+		+	+	+	+
Tanacetum vulgare L.	+							
Artemisia biennis Willd.	+		+					
A. vulgaris L.	+	+	+					
A. absinthium L.	+							
Senecio vulgaris L.	+							
S. ampullaceus Hook.		+						
Arctium minus (Hill) Bernh.	+	+	+	+	+	+		+
Carduus nutans L.	+	+	+	+	+	+		+
Cirsium vulgare (Savi) Ten.	+	+	+	+	+	+		+
C. arvense (L.) Scop.	+	+			+			+
C. texanum Buckley					+			
Centaurea solstitialis L.	+							
C. diffusa Lam.	+							
C. cyanus L.	+	+	+	+	+	+	+	+
C. nigra L.		+						
C. stoebe L. subsp. *stoebe*		+						
C. maculosa Lam.					+			
C. diluta Ait.			+					
Cichorium intybus L. f. *intybus*	+	+	+	+	+	+	+	+
f. *albus* Neum.					+			
Hypochaeris radicata L.	+							
Picris hieracioides L.				+				
P. echioides L.			+					
Tragopogon pratensis L.					+			
T. dubius Scop.	+	+	+	+	+	+	+	+
Taraxacum officinale Weber	+	+	+	+	+	+	+	+
Sonchus arvensis L. var. *glabrescens* Guenth.	+	+	+		+	+		
S. oleraceus L.	+	+	+	+	+	+	+	+
S. asper (L.) Hill	+	+	+	+	+	+	+	+
Lactuca serriola L.	+	+	+	+	+	+	+	+
L. saligna L.			+			+		
Crepis pulchra L.	+							
C. tectorum L.	+							

discussion. The degree of frequency is given as: common, frequent, scattered, rare. Widespread (occurrence in all 8 regions), or quite widespread (occurrence in 7 regions) is also indicated.

Persistence and naturalization is estimated. In cases of accepted persistence the first and the last years when the plant in question was seen are given. In many cases no records exist for some intermediate years, usually because the location was not visited in those years. The discussion of each species, with the exception of most of the ergasiophygophytes, ends with a reference to its origin. Numerous adventive botanists have given detailed descriptions of the native as well as the adventive occurrences of observed plants, but I believe that this does

not make much sense now, as one often has to reckon with second- and third-hand or further-removed introductions. Therefore, with some exceptions, continents only are mentioned. Mostly the data of *Gray's Manual of Botany* and Komarov's (1933–1964) *Flora of the U.S.S.R.* are used. For quite a few species the place of origin is uncertain. Some are cosmopolitan, spread more or less over the whole world, and for this reason there is disagreement about their original distribution.

GRAMINEAE

Bromus inermis Leyss.

Widespread, locally scattered, persisting in many places. One unusual case greatly helped expansion of this species. During the last decade the U.S. Corps of Engineers built the St. Louis floodwall which, for the most part, runs along the railroad. It is a stone structure to which an earth embankment was added in some places, especially along roadways leading to the railroad. In such places grew huge, luxuriant colonies of this species. An inquiry to the headquarters confirmed the suspicion that the slopes there were sown. The seed mixture used was over 50% "Smooth Brome Grass (southern strain)" by weight. Naturalized. Eurasia.

Bromus unioloides Kunth (*B. catharticus* Vahl)

Rare, observed in 2 regions in 6 localities 16 times, mostly as a few or even 1 or 2 specimens. There was a tendency to reappear in the same locality after it was missed for a year or so. The longest observation period was 7 years. Repeated introductions are less likely to have occurred rather than the failure of germination. Seen last in 1963. South America.

The next four *Bromus* species presented many difficulties in identification. Hitchcock (1950) already pointed out that some of these species are differentiated only by arbitrary characters. All doubtful *Bromus* material was sent for determination to H. Scholz (Berlin). See also his latest treatment (Scholz, 1970). The collections were made at random to get different looking specimens. With the exception of *B. squarrosus*, all species were frequent or scattered, *B. commutatus* being the most widespread. All four species are of Eurasiatic origin.

Bromus secalinus L.

Scattered, observed in 5 regions.

Bromus japonicus Thunb.

Quite widespread, locally frequent, almost half of the collections belong to subsp. **subsquarrosus** (Borb.) Pénzes.

Bromus commutatus Schrad. (*B. racemosus* L.)

Widespread, locally frequent.

Bromus squarrosus L.

M 954, 17 June 1956, 1 specimen. *M 1255B*, 4 July 1957, 2 specimens.

Bromus rigidus Roth

M 614, 30 May 1955, 1 specimen. Eurasia.

Bromus tectorum L.

Widespread, locally common, frequently in large pure stands with high density. Flowering begins in mid April; the last stragglers can be seen in August. Then the plant, which is so dominant in June and July, disappears almost completely. Naturalized. Eurasia.

Festuca rubra L. var. *commutata* Gaudin

M 1415, 7 June 1958, 1 small colony. *M 1430*, 28 June 1958, 1 large tuft. Northeastern U.S. and Eurasia.

Festuca pratensis Huds. (*F. elatior* L.)

Unexpectedly rare, found 14 times, including 6 unicates, in 5 regions. No persistence was ever observed. Eurasia.

Festuca arundinacea Schreb.

Widespread, locally frequent. Apparently strongly expanding; almost pure and persistent stands have developed on quite a few large, weedy, open lots and on margins of the railroad right-of-ways and the yards, but it was quite seldom found on the tracks. It is sometimes not recognized as a species because of intergradation with *F. pratensis*. Fernald (1950) does not mention it at all, but Pohl (1966) and Terrell (1968), among others, recognize both. *Festuca arundinacea* is considerably taller. One character deserves to be emphasized—the lowest branch of the inflorescence bears 1–2 spikelets in *F. elatior*, but (3–)5–8(–20) in *F. arundinacea*. Naturalized. Europe.

Festuca myuros L.

M 928, 9 June 1956, 1 specimen; *M 1194*, 2 June 1957, 1 colony. *M* 949, 17 June 1956, 1 specimen. Eurasia.

Puccinellia distans (L.) Parl.

M 70, 23 May 1954, 2 specimens. Eurasia.

Puccinellia airoides (Nutt.) Wats. & Coult.

M 1179, 1 June 1957, 2 specimens. Western U.S.

Poa annua L.

M 880, 5 May 1956, 1 colony. *M 1192*, 2 June 1957, few specimens. *M 1939*, 13 May 1962, 1 colony. *M 3246*, 15 May 1970, 1 colony. Unexpectedly rare, now and then mistaken for the more frequent native *P. chapmaniana* Scribn. Eurasia.

Poa compressa L.

Widespread, locally scattered, always in dense colonies and in many places persistent. Naturalized. Eurasia.

Dactylis glomerata L.

Widespread, common locally, sometimes the colonies were huge. Naturalized. Eurasia.

Eragrostis curtipedicellata Buckley

M 1993, Lindenwood Fr. Yd., 23 July 1962, 1 small colony. Not a new, but now a certain adventive for Missouri. Steyermark (1963: 107, 112) excluded this species from the *Flora of Missouri*. The new collection was determined by L. H. Harvey. According to him, the range of this prairie species is from southern Kansas to Coahuila, Mexico, and it has not been reported previously as a waif in railroad yards.

Eragrostis oxylepis (Torr.) Torr.

M 1931, 29 Oct. 1961, 1 small colony. Although several plants were left and no direct threats to its survival were apparent, no trace of this plant could be detected the next year. Southern and western U.S.

[*Eragrostis pilosa* (L.) Beauv.]

Cited in the *Flora of Missouri*, p. 107, it is, according to L. H. Harvey, the native *E. pectinacea* (Michx.) Nees.

Eragrostis multicaulis Steud.

M 3723, TRRA, E of Geraldine Ave., 3 Nov. 1971, 1 specimen. Determined by L. H. Harvey. According to Harvey, it is the first report of this Eurasian species from the Mississippi Valley. It is rapidly spreading in the northeastern U.S.

Eragrostis cilianensis (All.) E. Mosher (*E. megastachya* (Koel.) Link)

Widespread, locally scattered. In the juvenile stage it is difficult to distinguish from the next species. Steyermark (1963) described *E. cilianensis* as much more common in the state than *E. minor*. However, just the opposite is true in the St. Louis railroads. Eurasia.

Eragrostis minor Host

Widespread, locally frequent. Its colonies were often huge, but many specimens were dwarf. Naturalized. Eurasia.

Eragrostis barrelieri Daveau

M 2732, K Line Fr. Yd., 18 Sep. 1966, 1 large tuft. *M 3071*, Bremen Fr. Yd., 31 Oct. 1968, 2 tufts. Determined by L. H. Harvey. South European, it has already been found in quite a few southwestern states.

Eragrostis elliottii S. Wats.

M 3183, St. Louis Ave. Fr. Yd., 4 Oct. 1969, 1 specimen. Determined by L. H. Harvey. According to Harvey, its range includes the Gulf and Atlantic Coastal Plain states; also, no other reports about its occurrence as waif in railroad yards are known.

Eragrostis curvula (Schrad.) Nees

M 2955, 4 July 1968, 1 tuft. Of South African origin, according to L. H. Harvey, and planted for pasture and for erosion control on road cuts in the Southeast and Southwest. In St. Louis it is most likely an introduction.

Cynosurus echinatus L.

M 1628, 5 June 1960, 1 specimen. Eurasia.

Agropyron desertorum (Fisch.) Schult.

M 2471, St. Louis Ave. Fr. Yd., 31 May 1965, 1 large specimen. Determined by R. W. Pohl. According to Hitchcock (1950), extensively planted in the northern Great Plains area and found in grain fields in quite a few northwestern states. Introduced from Russia.

Agropyron repens (L.) Beauv.

Widespread, locally scattered, always in quite dense colonies but not especially large in extent. Naturalized. Europe, also along the North Atlantic coast of U.S.

Agropyron elongatum (Host) Beauv.

M 2956, Lesperance St. Fr. Yd. (MP), 4 July 1968, 1 small tuft. Determined by R. W. Pohl. Grown with success in the Wyoming Agricultural Experiment Station (Beetle, 1955). Eurasia.

Aegilops cylindrica Host

Widespread, locally scattered, mostly in small colonies, although sometimes, especially in the first years of the study, only a few or even unicate specimens were seen. Naturalized. Eurasia.

Lolium perenne L.

Rare, only 8 collections in 4 regions. In Missouri as a whole *L. perenne* and *L. multiflorum* are equally frequent (Steyermark, 1963), but in the St. Louis railroads *L. perenne* is much rarer than *L. multiflorum*. Eurasia.

Lolium multiflorum Lam.

Widespread, locally frequent, mostly in colonies, especially on margins, but also on the tracks. Sometimes sown (E of the Pickrel Fr. Yd. 1971) on bare slopes and embankments after construction. Naturalized. Eurasia.

[*Lolium temulentum* L. var. *temulentum*]

Cited in the *Flora of Missouri*, p. 136, it is, according to G. Davidse, *L. persicum* Boiss. & Hohen.

[*Lolium temulentum* L. var. *macrochaeton* A. Br.]

Cited in the *Flora of Missouri*, p. 136, it is, according to H. Scholz, *L. rigidum* Gaudin.

Lolium persicum Boiss. & Hohen.

Rare, observed in 2 regions 6 times, on 2 occasions several colonies at a time. It is a true ephemerophyte, never appearing the next year. Asia.

Lolium rigidum Gaudin

M 1411, Lesperance St. Fr. Yd. (MP), 7 June 1958, 1 specimen. Determined by H. Scholz. It is a monstrosity, sometimes also found in *L. perenne*. The spikes are, for the most part, branched. Eurasia.

Hordeum jubatum L. var. *caespitosum* (Scribn.) Hitchc.

M 995, 4 July 1956, 4 specimens. The typical variety is native to Missouri and

widespread on the railroad. The range of the introduced variety is, according to Hitchcock (1950), North Dakota to Alaska, south to California and Arizona.

Hordeum vulgare L.

Quite widespread, locally scattered, even rare in the beginning of this study. Among the cultivated grains observed on the railroad, barley was the rarest. Mostly on the tracks as a few specimens, but sometimes as unicates or colonies.

Triticum aestivum L.

The most common of the cultivated grain cereals on the railroad. It frequently grew in large colonies; the surroundings of some grain elevators were especially rich, but wheat also grew in quantity along many classification tracks. It was common to see mounds of wheat grain lying along the tracks, and this often attracted clouds of pigeon.

Secale cereale L.

It was the second most frequently found cultivated grain. Although widespread, rye was much rarer than wheat but behaved much the same on the railroad.

Holcus lanatus L.

M 1637, 5 June 1960; *M 1670*, 17 July 1960, both as a few specimens. *M 2948*, 4 July 1968, 3 specimens. Eurasia.

Avena fatua L.

Widespread, locally scattered, in many cases found as unicates. Eurasia.

Avena sativa L.

Widespread, more frequent locally than the previous species. Oats were less common than wheat and rye but were decidedly more frequent than barley.

Aira elegans Willd.

M 885, 13 May 1956, 1 colony. It was later destroyed by construction work. Eurasia.

Apera spica-venti (L.) Beauv. (*Agrostis spica-venti* L.)

This is a rapidly spreading plant, although not over the entire railroad area. First discovered on 5 June 1954 in Region 2 (*M 112*), the next year it was collected 8 times in Regions 1–4 along the Mississippi River. The center of the expansion was apparently the North St. Louis Yd., which is quite near the site of the original colony. In later years it was rated here as a common plant. *Apera spica-venti* also grew in the neighboring yards (Luther, Baden, Harlem, Carrie Ave., Bremen), but it was not as common. It advanced south as well, but showed no tendency to move along the western lines. It was found only once in Region 5. Naturalized. Eurasia.

Apera interrupta (L.) Beauv. (*Agrostis interrupta* L.)

M 1959, 30 May 1962, 1 colony. Eurasia.

Crypsis schoenoides (L.) Lam.

M 668, 4 July 1955, 1 colony, also observed 11 Aug. 1957 and 7 Sep. 1958. *M 1089*,

15 Sep. 1956, 1 colony. Also observed SL-SF, 39th St., 17 July 1955, 1 specimen. TRRA north of North Market St., 20 Aug. 1955, 1 specimen. N&W, Luther Fr. Yd., 28 Aug. 1955. It is remarkable that after this plant was found from 1955 to 1958 in 5 localities and in one of these localities for several years, it was never observed again after 1959. In spite of its small size, this grass is quite conspicuous, and it is hardly conceivable that it would later be constantly overlooked. Europe.

Phleum pratense L.

Widespread, locally frequent, always in colonies but mostly of modest size. Suspiciously frequent on the embankment of the St. Louis floodwall, but it could not be ascertained whether this frequently cultivated grass had also been intentionally sown there. Naturalized. Eurasia.

Cynodon dactylon (L.) Pers.

Widespread, locally scattered, remarkable were the huge, persistent colonies, sometimes in almost pure stands. It occurred mostly on the margins and open plots of the yards or along trunk lines, but rarely on the tracks. Bermuda grass is frequently used in lawns, so there is the possibility that at least in some cases it was only a garden escape. Naturalized. Eurasia.

Chloris virgata Swartz

M 1002, 8 July 1956, 1 specimen. Southern and western U.S.

Eleusine indica (L.) Gaertn.

Widespread, locally frequent. The distribution of this grass on the railroads in St. Louis is very unusual and curious; it was found almost completely on and along the many streets and roads which traverse the freight yards. Only in a few cases was it found on tracks far away from roads. This grass is frequent on the streets and sidewalks of the city, where it endures trampling very well. It is evident that this grass is spread by trucks and not by railroad traffic. See also Frenkel (1970) for the dissemination of ruderals in California by trucks. Naturalized. Tropical Asia and Africa.

Leptochloa dubia (H.B.K.) Nees

M 2407, Lesperance St. Fr. Yd. (MP), 1 Aug. 1964, 1 small colony. Determined by L. H. Harvey. Southern and western U.S.

Phalaris canariensis L.

Rare, observed in 4 regions 8 times, mostly 1–3 specimens, sometimes as small colonies. Last seen 1964. Europe.

Anthoxanthum odoratum L.

M 3313, 21 June 1970, few specimens. Eurasia.

Digitaria ischaemum (Schreb.) Schreb. ex Muhl.

Although found in all 8 regions, the plant could by no means be called common or even frequent. Its occurrence was very often as rare, and it was frequently found only as 1 or 2 specimens. It began to flower especially late in the season, mostly in September (only once at the end of July). Europe.

Digitaria sanguinalis (L.) Scop.

Widespread, locally common. Possibly the most frequent adventive, occurring almost everywhere. It began to flower quite late, in comparison with many other grasses, usually in the last quarter of June, or rarely in the first week of June. It continued to flower into November. Naturalized. Eurasia.

Eriochloa contracta Hitchc.

M 1066, 3 Sep. 1956, 1 colony. *M 3163*, 28 Sep. 1969, 1 colony; *M 3645*, 29 July 1971, 1 colony; *M 3687*, 2 Oct. 1971, 2 specimens. Southern and western U.S.

Paspalum dilatatum Poir.

M 1355, 8 Sep. 1957, also observed 26 July 1958; *M1478*, Sep. 1958, all several specimens. *M 2557*, 26 Sep. 1965, 1 specimen. South America.

Paspalum urvillei Steud.

M 1848, 9 Sep. 1961, 1 huge tuft. *M 3070*, 31 Oct. 1968, 1 large tuft. South America.

Panicum geminatum Forsk. (*Paspalidium geminatum* (Forsk.) Stapf)

M 1246, 30 June 1957; *M 1354*, 8 Sep. 1957; *M 1478*, 1 Sep. 1958, all the same plant. Southern U.S.

Panicum texanum Buckley

M 517, 22 Oct. 1954, few specimens. Southern U.S.

Panicum miliaceum L.

Rare, observed in 4 regions 10 times, in the majority (6) of cases as unicates. Broomcorn millet is cultivated to a limited extent in the cooler parts of the U.S., but not in Missouri. In St. Louis it is therefore not an escape, but a true adventive.

Echinochloa colonum (L.) Link

M 224, 5 July 1954, 1 small colony, also observed July–Sep. 1955. *M 1688*, 14 Aug. 1960, 1 specimen. *M 2400*, 26 July 1964, 1 colony. *M 2421*, 16 Aug. 1964, 1 specimen. *M 3186*, 5 Oct. 1969, 3 specimens. Tropical regions of both hemispheres.

Echinochloa crusgalli (L.) Beauv.

Widespread, locally frequent, almost always in colonies of moderate size, only 3 unicates recorded. Besides the typical form, f. *longiseta* (Trin.) Farw. was collected in all regions, but its occurrence was quite scanty. Naturalized. Eurasia.

Setaria glauca (L.) Beauv. (S. *lutescens* (Weigel) Hubb.)

Widespread, locally scattered, almost always in colonies of moderate or small size, only 3 unicates seen. Among the weedy Setarias this was the rarest species. Naturalized. Eurasia.

Setaria verticillata (L.) Beauv. var. *verticillata*

Quite widespread, locally scattered, almost always in colonies of different sizes, only once as a unicate. This species grew abundantly along buildings, including

those which border the tracks, but it was missing from the tracks themselves. Naturalized. Eurasia. Very rare was var. *ambigua* (Guss.) Parl. *M1295*, 4 Aug. 1957, few specimens. *M 1581*, 12 Sep. 1959, 1 specimen. *M 2545*, 19 Sep. 1965, 3 specimens. In the U.S. this variety is sometimes considered to be a hybrid between S. *verticillata* and S. *viridis*, but Hegi (1908–1931, 1935–1974) considers it a species. Eurasia.

Setaria viridis (L.) Beauv.

Widespread and common everywhere. This species plus *Bromus tectorum* and *Digitaria sanguinalis* were the most common adventive plants on the railroads. Its dominance began to show quite late, at the end of June, although a few plants could occasionally be seen a month earlier. This grass thrived until frost. Naturalized. Variety **major** (Gaudin) Posp. has been collected once, *M 2717*, TRRA, Third St. and Wharf, 17 Sep. 1966, 1 specimen. Determined by R. W. Pohl. Eurasia.

Setaria faberi Herrm.

Widespread, locally frequent on the tracks as well as on the margins, open lots, and along trunk lines, sometimes the colonies were gigantic. Apparently expending, as throughout the state (Steyermark, 1963). Naturalized. Asia.

Setaria italica (L.) Beauv.

M 1032, 4 Aug. 1956, 2 specimens. *M 1068*, 8 Sep. 1956, 1 specimen. *M 2665*, 9 July 1966, a large colony. Eurasia.

Pennisetum ciliare (L.) Link

M 1704, 18 Sep. 1960, ca. 6 specimens. India and Africa.

Miscanthus sinensis Anderss.

M 822A, 1 Oct. 1955, 1 huge tuft. *M 860*, 27 Nov. 1955, 1 huge tuft; *M 1131*, 20 Oct. 1956. *M 1906*, 8 Oct. 1961, 1 huge tuft. *M 2039*, 29 Sep. 1962, 1 huge tuft. This grass began to flower very late, mostly in October. Undisturbed, this plant would be obviously persistent, but it was destroyed in all localities.

[*Miscanthus floridulus* (Lab.) Warb.]

Cited in the *Flora of Missouri*, p. 241, it is, according to T. Koyama, *M. sinensis* Anderss. It was actually originally published under the latter name as a novelty for the Missouri flora (Mühlenbach, 1957).

Erianthus ravennae (L.) Beauv.

M 500, 17 Oct. 1954, 2 huge tufts. Observed for three years, it was then destroyed by bulldozing the whole area. South Europe.

Sorghum halepense (L.) Pers.

Widespread, locally frequent, in large, often huge, dense and persistent stands. Naturalized. Eurasia.

Sorghum bicolor (L.) Moench

Quite widespread, locally scattered, mostly in colonies of modest size, but unicates

not rare (15). Surely several varieties or races of the cultivated *Sorghum* were represented, but no attempts were made to more closely distinguish them. The preferred site was around the grain elevators.

Sorghum dochna (Forsk.) Snowden var. *technicum* (Koern.) Snowden
M 711, 6 Aug. 1955, few specimens (discovered by E. Anderson). *M 1105*, 29 Sep. 1956, 1 colony. Curiously enough, quantities of old brooms lay around on the ground, but they could hardly be the source of the colony.

Zea mays L.
Its occurrence was much like that of *Sorghum bicolor*, perhaps a little more frequent, and it was discovered in all regions. Its predilection for the surroundings of grain elevators was also obvious. Heaps of maize seeds on the ground there, and along many classification tracks, were striking sights.

CYPERACEAE

Carex nebraskensis Dewey
M 1199, 15 June 1957, 1 specimen. Southern and western U.S.

COMMELINACEAE

Commelina communis L.
Widespread, locally scattered, always in small colonies. Found primarily in shady places, frequently under bushes on the margins of the yards. Rarely, colonies were on the tracks in full sun, where the bulk of adventives used to thrive. Naturalized. Asia.

JUNCACEAE

Juncus gerardii Loisel.
M 2356, 14 June 1964; *M 2505*, 24 June 1965; *M 2522*, 29 Aug. 1965; *M. 2625*, 3 June 1966. In the following years it appeared constantly through 1971; when discovered, there were two dense colonies which later merged into one. A 1966 fire destroyed the surrounding vegetation far and wide, but this species persisted. Eurasia.

LILIACEAE

Allium sativum L.
Quite widespread, locally rare, observed 14 times, always in small colonies on the margins of the yards or along trunk lines, in a few places persisting for some years. Probably at least in part a garden escape.

Allium vineale L.
Widespread, locally frequent, always in colonies. Twice f. *compactum* (Thuill.) Aschers. was found (only bulblets instead of flowers in the umbels): *M 618*, 30 May 1955, rare. *M 3284*, 6 June 1970, 2 colonies. Naturalized. Eurasia.

Allium cepa L.

Onion bulbs with developed sterile sprouts are infrequently met, especially around the St. Louis Produce Market, but only twice were flowering specimens collected. First, var. *viviparum* Metz was found: *M 1165*, 30 May 1957, 2 specimens. Later var. **cepa**: *M 3100*, St. Louis Ave. Fr. Yd., 21 June 1969, 1 specimen. Determined by H. Cutler.

Hemerocallis fulva L.

It was found in all regions, but was locally quite rare. It occurred on the margins of the yards and right-of-ways. In some places it was surely persistent, possibly in most cases as an escape; however, some localities were far away from gardens. Very rare is var. *kwanso* Regel (in Regions 1, 4, 8). Eurasia.

Ornithogalum umbellatum L.

M 1144, 5 May 1957, 1 colony. *M 2331*, 10 May 1964, 1 dense tuft (UMO). Most probably a garden escape. Eurasia.

Muscari botryoides (L.) Mill.

M 3221, 25 Apr. 1970, 1 small colony near heaps of grass clippings which most probably contributed to the occurrence of this ornamental here. Europe.

Yucca filamentosa L.

M 777, 11 Sep. 1955, 1 sterile specimen. It was afterwards destroyed. According to F. G. Meyer, who determined the collection, it is near *Yucca smalliana* Fern., which has already been found in Missouri. Most likely a garden escape. Coastal Plains, Georgia to New Jersey.

Asparagus officinalis L.

Thus cultigen was quite widespread, locally scattered. It grew mostly along margins and on open lots, infrequently on tracks. Many localities were far from gardens. Sometimes flowering recurred very late in the autumn (November).

AMARYLLIDACEAE

Narcissus × biflorus Curtis (*N. poeticus* L. × *tazetta* L.)

M 3503, MP, southeast of Morganford Rd., 24 Apr. 1971, 2 large tufts. Determined by F. G. Meyer. The plant was noted already in 1970, but then considered to be an ergasiophyte. Later inquiries in the neighborhood proved that no plantings had ever been made on the siding in question. Therefore *N. biflorus* can be interpreted as belonging to the scope of this study.

IRIDACEAE

Iris germanica L.

M 530, 30 Apr. 1955, 1 specimen. *M 2323*, 2 May 1964; *M 2453C*, 8 May 1965, 1 very dense colony or a huge specimen. It disappeared, after two years, possibly having been dug out for transplantation. *M 3260*, 17 May 1970, small colony. *M 3507*, 24 Apr. 1971, 2 colonies. Surely a garden escape. *Iris* species were

observed quite a few other times, but in circumstances which gave reason to believe that they were only remnants of intentional plantings (ergasiolipophytes).

ULMACEAE

Ulmus pumila L.

Widespread, locally scattered, mostly in isolated specimens on margins and open lots, rarely on the tracks. In the overwhelming majority the shrubs were low (0.5–2 m). The shrubs were, with few exceptions, sterile. Flowering and fruiting specimens were collected only thrice from older and taller shrubs. Determined by J. W. Thieret. Similar looking shrubs are frequent on St. Louis streets, especially in the alleys. Naturalized. Asia.

MORACEAE

Morus alba L.

Widespread, locally scattered, mostly in small colonies, its distribution was similar to the preceding species, except that small, crippled specimens occasionally could be found on the tracks also, even with frequent traffic. The fruits were, in the vast majority of cases, purplish violet, seldom yellowish. Naturalized. Asia.

Broussonetia papyrifera (L.) Vent.

M 3518, 9 May 1971, several tall trees as well as low shrubs in a small grove, first noticed 20 Sep. 1970. Apparently a well-established colony, but the locality could be easily wiped out by some industrial development of the terrain. Asia.

Maclura pomifera (Raf.) Schneid.

Scattered, observed in 6 regions, especially along some trunk lines where a woody vegetation accompanied the tracks. In such places some trees can reach a respectable height. Low shrubs were rarely found on tracks. Steyermark (1963) evaluated its status as introduced and naturalized in Missouri. Southwestern U.S.

CANNABINACEAE

Cannabis sativa L.

M 255, 17 Sept. 1954, 1 colony. It reappeared until 1964. At this time the colony was apparently discovered by the authorities, who regularly began to cut the plants down. The colony was completely destroyed by 1966. *M 1305*, 17 Aug. 1957, 1 small colony. Also observed MP, Spring Ave. and Vandeventer, 14 July 1963, 1 small colony, but spread over a larger area. At the three last localities, no trace could be found of *C. sativa* in the following years. Eurasia.

Humulus japonicus Sieb. & Zucc.

Widespread, locally scattered in big persistent colonies on the margins of the yards and right-of-ways, for the most part twining on different shrubs or fences, rarely, lying directly on the ground without any support, especially in Region 7, where the tops sometimes reached the rail of the track. Naturalized. Asia.

POLYGONACEAE

Rumex patientia L.

Widespread, locally frequent in large, persistent colonies. Naturalized. Eurasia.

Rumex crispus L.

Widespread, but as contrasted with the previous species, much rarer locally, developing only small colonies or occurring as a few specimens or even as unicates. Steyermark (1963) noted that this species probably occurs in every county in Missouri, while the preceding species was known from only 4 counties. This is a good example of how differently two related species can be distributed on a local and state-wide scale.

Rumex pulcher L.

M 957, 17 June 1956, 1 specimen. *M 1261*, 7 July 1957, 2 specimens. *M 1422*, 28 June 1958, 1 specimen. *M 1638*, 18 June 1960, 1 small colony. Eurasia.

Rumex obtusifolius L.

Rare, observed in 4 regions 19 times. It is likely that in several cases the same colony was repeatedly recorded in the same season. The colonies were small, in some places persisting for several years. Unicates were also observed. Eurasia.

Rumex stenophyllus Ledeb.

Possibly rare, observed in 4 regions 11 times, 6 of which were unicates, but the plant was probably much more frequent. It was recognized very late in this study. A *Rumex* collected in 1967 was sent to H. A. Wahl because it seemed to be a *R. crispus* × *R. obtusifolius* hybrid. H. A. Wahl determined it as *R. stenophyllus*; thereafter much more attention was later paid to *Rumex* species, and this species was then discovered in other localities. Steyermark (1963), also noted the resemblance of this species to a hybrid between *R. crispus* and *R. obtusifolius*. Eurasia.

Rumex dentatus L.

M 2821, North St. Louis Fr. Yd., 25 June 1967; *M & D'Arcy 3195*, 16 Oct. 1969; *M 3205*, 5 Dec. 1969, all the same plant. This annual plant persisted at the same spot for two years. In 1970 the entire area was covered with heaps of rubbish, and in 1971 a thorough bulldozing was performed, no doubt destroying the plant. Determined by C. Frankton and confirmed by K. H. Rechinger. Asia.

Rumex acetosella L.

Widespread, locally scattered, in many places persistent, always in colonies of modest size. Naturalized. Europe.

Polygonum pensylvanicum L. var. *rosaeflorum* J. B. S. Norton

M 2222, 15 Sep. 1963, 1 specimen. *M 2275*, 12 Oct. 1963, 5 specimens. *M 2275*, 12 Oct. 1963, 5 specimens. *M 2914*, 4 Nov. 1967, 1 huge specimen. *M 3475*, 7 Nov. 1970, scattered. While the typical variety is widespread in the U.S., var. *rosaeflorum* is mentioned by Fernald (1950) as a native also, but only in the East (Delaware, Maryland and Virginia). In numerous floras of states between the

Atlantic coast and Missouri it is not mentioned, so it could well be an introduced plant in St. Louis.

Polygonum lapathifolium L. var. *prostratum* Wimm.

M 2150, 27 July 1963, 1 specimen. An introduced European variety of the common American species.

Polygonum scabrum Moench

M 2766, 23 Oct. 1966, 3 specimens. *M & D'Arcy 3083*, 29 May 1969, 1 specimen. Eurasia.

Polygonum orientale L.

M 1025, 22 July 1956, also observed 9 Sep. 1956, 1 specimen. Eurasia.

Polygonum cespitosum Blume var. *longisetum* (De Bruyn) Stewart

Scattered, observed in 5 regions. Locally always in colonies which were at least somewhat persistent. First collected 1963, but later showing a definite tendency to spread. The first records from Missouri dating from 1959 were from the city —along the sidewalk of Tower Grove Ave., outside the grounds of the Missouri Botanical Garden (Steyermark, 1963). It is well known that many botanical gardens have played prominent roles in the introductions of plants. With their help a long series of plants, some of them noxious from an economical point of view, were spread, first in the immediate vicinities of the gardens, and later through whole countries. *Polygonum cespitosum* has been for years a frequent weed in the Missouri Botanical Garden, but the exact time of its appearance is not known.[11] Also unknown is the primary source of this plant. Has it advanced into the Garden from the street, or vice versa? Nowadays it appears frequently in the city. Naturalized. Asia.

Polygonum persicaria L.

Widespread, locally also often seen. Possibly it is even more frequent than records show. Several common or frequent native Polygonums look quite similar, but it would make little sense to investigate more closely every *Polygonum*. Naturalized. The white flowered f. *albiflora* Millsp. was also collected, *M 2695*, 2 Aug. 1966, 1 colony. *M 2731*, 18 Sep. 1966, 1 colony. (H. A. Wahl did a progeny test on the second collection, his no. P875, 27 July 1967.) Eurasia.

Polygonum convolvulus L.

Widespread, locally at least scattered, if not frequent. It is one of the least visible adventives and can be easily overlooked. Naturalized. Eurasia.

Polygonum cuspidatum Sieb. & Zucc.

Quite widespread, locally scattered, developing a few huge colonies on different open lots. Naturalized. In the Carrie Ave. Fr. Yd. (RI) a large colony was discovered in 1955; it flourished undisturbed through 1969. In 1970 the whole area was bulldozed to convert it into a parking lot for piggy-back trucks. Already

[11] The oldest specimen in the herbarium of the Garden is from 1965.

that autumn many sprouts appeared and it even seemed that the perimeter of the colony had enlarged—the bulldozing must have conveyed the rhizomes around. By 1971 the colony was established again. Japan.

Fagopyrum sagittatum Gilib.

Rare, observed in 5 regions 14 times, in the majority of cases only as 1–2 specimens. When colonies were observed, they were small. On tracks as well as along a seed company's warehouse.

CHENOPODIACEAE

Kochia scoparia (L.) Schrad.

Widespread, locally abundant. It was one of the most common adventives in St. Louis. In the American literature it is mostly viewed as an escape from cultivation, which seems debatable to me. Rather, Swing (1969) hit the nail on the head by calling *K. scoparia* "a very common weed" in his flora of the Chicago region, later adding, "The increase of the plant has been phenomenal." Hegi mentions that it is cultivated here and there in Middle Europe, but the description of localities (at least in Germany) seems to speak for introductions. Besides, the cultigen is mostly the variety which is not observed here or is possibly overlooked in the mass of the typical variety of this species. It is dominant in the second half of the summer. Naturalized. Eurasia.

Kochia iranica (Hausskn. & Bornm.) Litw.

M 2263, Baden Fr. Yd., 6 Oct. 1963, 1 specimen. Determined by W. A. Weber. Asia.

Chenopodium murale L.

M 1560, 2 Aug. 1959; *M 1727*, 5 Nov. 1960; *M 2306*, 26 Oct. 1963; always only a few specimens. *M 1657*, 4 July 1960, 4 specimens. *M 2308D*, 27 Oct. 1963, 1 specimen. Eurasia.

Chenopodium botrys L.

Although observed in 7 regions it must be considered rare. Most of the 24 finds were in the first three years, especially in Region 3. In later years it was very sporadic; in many years missing altogether. It was found for the last time in 1967. Only small colonies had developed and quite a few unicates (5) were observed. Eurasia.

Chenopodium ambrosioides L.

Quite widespread, locally frequent. Among the adventive Chenopodiums, it was the most frequent. It grew mostly in large, even huge, colonies, sometimes in almost pure stands, infrequently on the tracks. Naturalized. Tropical America.

Chenopodium pumilio R. Br.

M 937, 16 June 1956, 10–15 specimens, seen several times afterwards through 1958, although not on exactly the same spot. *M 2244*, 29 Sep. 1963, 2 specimens. Australia.

Chenopodium glaucum L. var. *glaucum*

M 975A, 30 June 1956, 1 specimen. *M 2859*, 5 Aug. 1967, 1 huge specimen. *M & D'Arcy 3082*, 29 May 1969, 1 specimen. Var. *salinum* (Standley) Boivin: *M 975B*, 30 June 1956, 1 specimen. The typical variety is native in the Old World (Eurasia), but var. *salinum* is native in the western U.S.

Chenopodium watsonii A. Nelson

M 1795, 1 July 1961, 1 specimen. Western U.S.

Chenopodium opulifolium Schrad.

M 3637, 27 July 1971, 1 specimen. Determined by J. P. M. Brenan and H. A. Wahl. This species, which must be considered a "good" one, is missing in Steyermark's *Flora of Missouri*, but in Correll & Johnston's *Manual of the Vascular Plants of Texas* is the following remark, ". . . Adv. at e. coast seaports from N.Y., N.J., Pa., Del. and Md.; also in Ill., Mo. and Tex." Several letters were of no help in discovering the primary source of the adventive occurrence of *C. opulifolium* in Missouri. Be that as it may, this species is not interpreted as a novelty to Missouri. Europe.

Atriplex rosea L.

M 1972, 16 June 1962, 1 specimen; *M 2401*, 26 July 1964; *M 2435*, 30 Aug. 1964, all the same plant. Although only parts of the plant were taken in 1964, it did not appear the following year. Eurasia.

Atriplex truncata (Torr.) Gray

M 974, 30 June 1956, 1 small colony, and 1 isolated specimen. *M 1521*, 7 June 1959; *M 2106*, 23 June 1963; *M 2210*, 15 Sep. 1963, all the same small colony. Although several specimens were left, no trace was found the following year. Western U.S.

[*Atriplex argentea* Nutt.]

Cited in the *Flora of Missouri*, p. 615, it is, according to H. A. Wahl and C. Frankton, *A. truncata* (Torr.) Gray.

Atriplex heterosperma Bunge

M 1026, 22 July 1956, 1 colony together with *A. hastata* L. The latter persisted through 1970, while no trace of *A. heterosperma* was later found. Eurasia.

Salsola kali L. var. *tenuifolia* Tausch

Observed in 6 regions, locally frequent, but by no means could it be considered a troublesome weed as has happened so frequently elsewhere. It usually grew in large, diffused, but apparently persistent, colonies with a preference for the tracks. Naturalized. Eurasia.

Salsola collina Pall.

Observed in 5 regions. The first collection was made in 1964. In the next few years it had to be considered a rarity, but since 1969 it began to appear more often. In 1971 it was quite frequent in the East Jefferson Fr. Yd. (TRRA). A rapid

expansion has apparently occurred. It occurs mostly with *S. kali*. Once (in November) seen as a tumbleweed. Eurasia.

Beta vulgaris L.

M 1963, 2 June 1962, 1 specimen. The root of the plant was remarkably thin. Komarov (1934–1964) also mentions that cultivated beets after escape may degenerate and produce a small, thin root.

AMARANTHACEAE

Celosia cristata L.

M 1334, far away from any garden, 1 Sep. 1957. *M 1364*, 14 Sep. 1957, 1 specimen. *M* 3688, 6 Oct. 1971, 3 specimens. Asia.

Amaranthus palmeri S. Wats.

Rare, collected in 6 regions 23 times. However, it is possible that this plant was more frequent, but was overlooked. *Amaranthus* is one of the most prevailing genera on the railroads in the autumn. Besides the 7 adventives, 4 native species are widely spread. Moreover, numerous hybrids in different combinations make the situation even more complicated. Therefore, this species, as well as most of the other adventive ones, may not be so rare as the collections indicate. It is also possible that some other adventive species which could occur here were not recognized. *Amaranthus palmeri* appeared in small colonies, frequently as a few or unicate specimens. Especially frequently collected in Region 1. Southern U.S.

Amaranthus arenicola I. M. Johnston (*A. torreyi* (Gray) Benth.)

M 228, 5 July 1954, 1 colony. *M 745*, 4 Sep. 1955. *M 1109*, 29 Sep. 1956, 1 specimen. *M* 2554, 25 Sep. 1965, 1 specimen. Southern and western U.S.

Amaranthus hybridus L.

Widespread, locally scattered, mostly in small colonies. Naturalized. According to many writers (including Steyermark, 1963), probably native of tropical America, while Sauer (1967) considers it indigenous in North America.

Amaranthus retroflexus L.

Widespread, locally common. Naturalized. The remarks about the possible origin are the same as for the previous species.

Amaranthus powelii S. Wats.

M 736, 28 Aug. 1955, 1 specimen. *M 1435*, 4 July 1958. *M* 2553, 25 Sep. 1965, 1 specimen. *M* 3587, 26 June 1971, 1 small colony. Southern and western U.S.

Amaranthus spinosus L.

Rare, observed in 4 regions 6 times. The records for the three most frequent *Amaranthus* species in Missouri show that their distribution in St. Louis is very different from that in the state. According to Steyermark (1963), *A. hybridus* is recorded from 34 counties, *A. retroflexus* from 21, and *A. spinosus* from 28, although he does not doubt that these species must actually be more common

than herbarium collections indicate. In St. Louis *A. retroflexus* is very common, but *A. spinosus* is rare, while *A. hybridus* falls in between. Possibly tropical America.

Amaranthus tricolor L.

M 3449, N&W, Era Ave. and Mimica Ave., 22 Oct. 1970, also observed 22 July 1971, 1 colony. Determined by J. D. Sauer. As in *Muscari bothryoides*, this ornamental was probably introduced with lawn clippings, dumped on the railroad. Possibly tropical Asia.

AIZOACEAE

Mollugo verticillata L.

Widespread, locally quite frequent, mostly in large but diffuse colonies. Naturalized. Tropical America.

PORTULACACEAE

Portulaca oleracea L.

Widespread, locally scattered, mostly in small, more or less diffuse, colonies or in some cases only as a few or unicate specimens. Naturalized. Asia.

Portulaca grandiflora Hook.

Rare, observed in 6 regions 30 times, in some localities repeatedly, mostly as a few or even unicate (9) specimens. In the case of one persistent colony the suspicion that it was a remnant of a previous planting (an ergasiolipophyte) could not be overcome. In other cases this plant was an ergasiophygophyte or escape, but some localities were on tracks, far away from gardens. The colors of the petals may be rose, red, or yellow (the most common). Sometimes all seen in the same colony. South America.

CARYOPHYLLACEAE

Arenaria serpyllifolia L.

Frequent, observed in 6 regions, often in large persistent colonies. Naturalized. Europe.

Stellaria media (L.) Cyrillo

Widespread, locally scattered, mostly in colonies of moderate size. Two facts are worth mentioning. First, *S. media* is much rarer on the railroads than in the city itself. Secondly, it is a vernal plant par excellence, flowering in April and May, or very seldom in June, and then disappearing completely. Towards the autumn (September) new sterile plants reappear here and there. Only once was a flowering colony detected in November. Eurasia, now cosmopolitan.

Cerastium holosteoides Fries subsp. *triviale* (Link) Möschl f. *glandulosum* (Boenn.) Möschl (*C. vulgatum* L.)

Rare, collected in 5 regions 9 times, always in small colonies. In one locality it was observed 4 years in succession. Eurasia.

Cerastium glomeratum Thuill. (*C. viscosum* L.)

M 3581, 24 June 1971, 1 specimen. Eurasia.

Cerastium semidecandrum L.

M 3520, 9 May 1971. *M 3524*, 9 May 1971. In both localities, near the MP elevator, 1 colony. This species was excluded by Steyermark (1963) from the *Flora of Missouri*. The new collections were determined by W. Möschl. Eurasia.

Cerastium pumilum Curtis

This is one of the most notable finds according to W. Möschl who determined all the *Cerastium* material. *Cerastium pumilum* has been collected 17 times in 7 regions, usually as f. *pumilum*, more rarely as f. **medium** Möschl. Apparently this species has at least in some cases been referred to the native *C. brachypodum* (Engelm.) Robins., which Möschl has also identified in a mixed colony with *C. pumilum*. *Cerastium pumilum* is considered to be a very rare adventive in the U.S. Its unexpected abundance here may perhaps be explained by previous failures in the distinction of the two species, as has been the case with *Delphinium consolida-D. ajacis* and *Torilis japonica-T. arvensis*. Europe.

Holosteum umbellatum L.

M 1132, 4 May 1957, observed through 1960. *M 2073*, 14 Apr. 1963. *M 3213*, 12 Apr. 1970. *M 3533*, 16 May 1971. In all localities colonies of different sizes. Eurasia.

Agrostemma githago L.

Quite widespread, locally scattered. The colonies were small, and it was frequently found only as a few specimens or unicates. One thing is striking; it is becoming much rarer, if recent findings are compared with those of the first years. It was recorded 16 times in 1955, 12 times in 1956, but only a single plant was observed in 1971 and none in 1970, although excursions in later years were more numerous than in the 1950s. Eurasia.

Lychnis alba Mill.

Scattered, but rare, observed in 5 regions, but like the previous species, apparently becoming rarer, having been observed 9 times in 1955, 8 times in 1956, but only 4 times in 1970. Mostly as a few or as unicate specimens, sometimes in quite large colonies. Infrequently a second flowering occurred in October. Eurasia.

Silene cucubalus Wibel

M 567, 8 May 1955, 1 specimen. *M 586*, 15 May 1955, 1 specimen. TRRA, Lesperance St. Fr. Yd., 26 June 1955, 2 specimens. MKT, Baden Fr. Yd., 22 June 1957, 2 specimens. In three localities the plant persisted for several years, in one place through 1960. A slight tendency for spreading was observed, but the plant nevertheless finally disappeared in all localities. Eurasia.

Silene cserei Baumg.

M 592, 22 May 1955, few specimens. *M 681*, 16 July 1955, 1 colony, observed

through 1963. TRRA, O'Fallon Fr. Yd., 26 May 1957, 1 specimen. MP, north of Nagel St., 29 June 1963, 1 large colony. According to Frankton & Mulligan (1974) it is a pest around railway installations in Canada. Europe.

Silene armeria L.

M 3451, N&W, Era Ave. and Mimica Ave., 22 Oct. 1970. Determined by F. Markgraf. By 20 May 1971 the colony had increased considerably in size. It was later destroyed. In the U.S. it is mostly cited as a garden escape, but Gleason (1968) described it also as "a weed in waste places almost throughout our range." Taking into consideration that the locality was on the trunk line of N&W with its numerous garden escapes, it seems reasonable to include it with the escapes. Eurasia (Fernald, 1950; but according to Komarov 1933–1964 in Asia only as an introduced plant).

Silene conoidea L.

Rare, observed in 3 regions (predominantly in one) 14 times. First one small colony was discovered; later, usually only unicates or two specimens were located. Eurasia.

Silene dichotoma Ehrh.

M 672, 9 July 1955, 1 specimen, heavily damaged by a weed killer, but still recognizable. Eurasia.

Silene gallica L.

M 2900, 28 Oct. 1967, 2 specimens. Half of a plant was left, but no trace of this species was found the next year. Eurasia.

Silene noctiflora L.

Rare, observed in 4 regions. On several occasions isolated specimens were dispersed over a whole yard, making it difficult to count localities, but in the vast majority of cases this plant appeared as unicates or two specimens. Often found on the tracks. Eurasia.

Saponaria officinalis L.

Widespread, locally frequent, usually in large colonies, but almost always only on margins or open lots. Only in exceptional cases was it found on the tracks, and then only as one or a few specimens. Naturalized. Eurasia.

Saponaria vaccaria L.

Rare, observed in 5 regions 40 times, in the majority of cases as unicates or as 2–3 specimens, very often on the tracks. Eurasia.

Dianthus armeria L.

Rare, locally observed in 4 regions 23 times, but in only 8 localities. In some places this plant was persistent for years. The longest observed time was 11 years. Partly in small colonies, or as 1–2 specimens. Europe.

RANUNCULACEAE

Ranunculus acris L.

M 923, 9 June 1956, 1 specimen (POM). Eurasia.

Ranunculus sardous Crantz

M 3280, 24 May 1970. *M* 3295, 9 June 1970, both 1 specimen. Europe.

Ranunculus arvensis L.

M 1537, 14 June 1959, 4 specimens. Although ripe achenes lay on the ground at the time of the discovery, no plants could be observed the next year. Eurasia.

Clematis dioscoreifolia Lévl. & Vaniot

M 343, 14 Aug. 1954. *M 487*, 9 Oct. 1954. *M 770*, 11 Sep. 1955. Observed in the first two localities through 1957 and 1956, respectively. Most probably a garden escape. Asia.

Delphinium ajacis L.

Widespread, locally scattered, mostly in more or less large colonies, but also as unicates, always only on margins and open lots. The colors of the flowers can be very different, even in the same colony, varying from dominantly blue to pink and white. It was persistent in many localities. Naturalized. It is most probably a garden escape. Europe.

Delphinium consolida L.

M 3106, Tyler St. Fr. Yd., 21 June 1970, 1 colony. Determined by F. Markgraf. Although several specimens were left, no trace of this conspicuous plant could be found in 1971, though the locality was very secluded and safe. Eurasia.

PAPAVERACEAE

Eschscholtzia californica Cham.

M 1788, 1 July 1961, 1 large colony, but few flowers were present (US). Pacific U.S.

Argemone albiflora Hornem.

M 669, 4 July 1955, ca. 6 specimens, observed through 1957. *M 1308*, 18 Aug. 1957, 2 specimens. Southern U.S.

CAPPARACEAE

Cleome hassleriana Chod. (*C. houtteana* Schlecht.)

M 2890, 2892, 7 and 28 Oct. 1967, 1 specimen. Surely a garden escape, probably through dumping. Latin America.

CRUCIFERAE

Berteroa incana (L.) DC.

M 616, 30 May 1955, 3 specimens. *M 1541*, 12 July 1959, 1 specimen. BN, North St. Louis Fr. Yd., 4 July 1961, 2 specimens, not taken, but later found destroyed. Eurasia.

Lobularia maritima (L.) Desv.

M 3450, N&W, Era Ave. and Mimica Ave., 22 Oct. 1970, 1 small colony. Deter-

mined by H. Scholz and R. L. Stuckey. Probably introduced by dumped lawn clippings. Europe.

Thlaspi arvense L.

Widespread, locally frequent in colonies of different sizes on margins as well on the tracks. It was prevalent in the first half of the summer until the end of June, more or less disappeared for a period, and then around of the first of September fresh flowering colonies reappeared but as rarities. Naturalized. Eurasia.

Lepidium perfoliatum L.

Rare, observed in 4 regions 26 times, seldom in large colonies, mostly as unicates (9) or as a few specimens. It was mostly found in Region 1, especially in the North St. Louis Yard (BN). The impression was that the localities where it was found were not constant. Naturalized.

Lepidium campestre (L.) R. Br.

Quite widespread, locally rare, observed 34 times, in the majority of cases as unicates, although several large colonies were found. This plant seemed to be becoming rarer. In 1971 it was not observed at all, only twice in 1970, and seven times in 1955. Short-dated persistence in a few localities. Eurasia.

Cardaria draba (L.) Desv.

M 15, 17 Apr. 1954. *M 1169*, 30 May 1957. In both localities large colonies which persisted through 1971. *M 3519*, 9 May 1971, 1 large colony, surely until then overlooked. After flowering this species disappeared quite quickly and completely. Although *C. draba* grew luxuriantly in one locality for 18 years (and E. Anderson knew of the existence of this colony for years before), I hesitate to call it naturalized. The first two colonies especially must be considered as growing in endangered sites, where they could be easily destroyed by unforeseen activities of the railroads. Eurasia.

Cardaria pubescens (C. A. Mey.) Rollins var. *elongata* Rollins

M 62, 23 May 1954, 1 specimen. Afterwards it was frequently found through 1970, but fluctuated strongly in number. The locality was quite endangered, a narrow strip between a track and a roadway, and often sprayed with weed killers. Curiously, there was no tendency to spread from that strip. *M 906*, 2 June 1956, 1 specimen seen several times, last seen 15 May 1960 as 1 small colony. *M 1227*, 22 June 1957, 1 small colony. Asia.

Capsella bursa-pastoris (L.) Medic.

Widespread, locally common, mostly in large, more or less diffuse, colonies. Flowering began early in the spring and extended until June. Then the plant disappeared completely, but rarely reappeared with flowers and fruits late in the autumn, the earliest at the end of September. Naturalized. Eurasia.

Camelina microcarpa Andrz.

Scattered, observed in 6 regions, as a few specimens or small colonies, chiefly on the tracks. Sometimes quite a few specimens were widely spread over a whole yard. Persistence could not be ascertained. Eurasia.

Neslia paniculata (L.) Desv.

M 1153, 26 May 1957, 1 specimen. *M 1183*, 1 June 1957, 2 specimens. *M 2640*, 18 June 1966; *M 2941*, 22 June 1968, 2 specimens. *M 3121*, 4 July 1969, twice 2 specimens. The last 3 localities were along a cleanout track. Eurasia.

Raphanus raphanistrum L.

Rare, observed in 5 regions 15 times, usually as unicates, only in a very secluded locality as a small colony which persisted to the following summer. In Europe it is one of the most common weeds, and Hegi (1908–1931) described it as occurring on suitable sites "everywhere." He also mentions its introduction into North America, noting that it is a troublesome weed, especially in the East. It, therefore, seems strange that this plant has not been able to gain a firm footing in St. Louis in spite of repeated introductions. Eurasia.

Raphanus sativus L.

Rare, observed in 2 regions 10 times, mostly as unicates. Last seen, 1963.

Brassica hirta Moench (*Sinapis alba* L.)

Rare, observed in 6 regions 14 times, mostly in colonies of different sizes. It is possible that it was, at least in part, an escape from cultivation. Eurasia.

Brassica kaber (DC.) L. C. Wheeler

Widespread, locally scattered, mostly in colonies of moderate size. Flowering ceased in June, reappeared in the autumn, but, as is usual with other plants having a second late flowering, only in a few isolated specimens. Like *Raphanus raphanistrum*, with which *B. kaber* is often confused, it is in Europe a common and troublesome weed. It seems that in St. Louis *B. kaber* has adapted much more successfully. Naturalized. Eurasia.

Brassica juncea (L.) Coss.

Quite rare, but possibly sometimes overlooked in the field, different *Brassica* species often looking quite similar in the field. Recorded in 6 regions 31 times, for the most part in small colonies, but also quite a few (7) unicates were seen. Much rarer was var. *crispifolia* Bailey (*B. japonica* Hort.): *M 646*, 18 June 1955, 1 specimen. *M 1269*, 7 July 1957, 1 specimen. *M 1417*, 7 June 1958, 1 small colony. Also MP, Biddle Fr. House, 26 July and 7 Sep. 1958, 1 colony. Eurasia.

Brassica nigra (L.) Koch

Rare, observed in 3 regions 15 times. In contrast to the other species of this genus, only small numbers of plants could be found, usually as unicates, occasionally as 2 or 3 specimens. Eurasia.

Brassica rapa L.

Rare, observed in 6 regions 23 times, mostly in colonies of modest size. Only in few cases did the plants seem to be escapes from cultivation. The vast majority represented the wild form, from which the cultigens are derived. Hegi (1908–1931) uses the name *Brassica campestris* L. s. str. Eurasia.

Brassica napus L. var. *napobrassica* (L.) Peterm.

M 879, 5 May 1956, 4 specimens. MRS, River Yard, 13 May 1956, 1 specimen (not taken).

Erucastrum gallicum (Willd.) O. E. Schulz

Rare, observed in 5 regions 30 times, prevalently as unicates, rarely as 3 or more specimens. The largest number were frequently found on the tracks. Europe.

Conringia orientalis (L.) Dumort.

Rare, observed in 5 regions 17 times, mostly as unicates, but occasionally as small colonies. No persistence was ever observed. Eurasia.

Sisymbrium officinale (L.) Scop. var. *leiocarpum* DC.

Rare, observed in 4 regions 13 times, in the majority of cases as unicates. Where colonies developed, they were small. Eurasia.

Sisymbrium altissimum L.

A frequent plant, although not observed in one of the regions. It often grew in huge colonies on the tracks, as well as on open lots and margins. This is another case of differential spreading by related species after introduction in Missouri. According to Steyermark (1963), *Sisymbrium officinale* is recorded much more often than S. *altissimum* in Missouri. In St. Louis the situation is just the opposite. Naturalized. Eurasia.

Sisymbrium loeselii L.

Rare, observed in 3 regions 11 times, once as 4 specimens, in all other cases the plants occurred as unicates. Eurasia.

Arabidopsis thaliana (L.) Heynh.

Rare, observed in 3 regions 6 times, always in large dense colonies. It is a vernal plant, flowering only in April and the first week of May. Eurasia.

Descurainia sophia (L.) Webb

Scattered, observed in 6 regions, mostly in colonies of different sizes, sometimes also as unicates, on the tracks as well as on margins or open lots. Whether the colonies are persistent or whether naturalization has already been achieved could not be unequivocally determined. Eurasia.

Erysimum repandum L.

Widespread, locally scattered, mostly in colonies of different sizes. It is a vernal plant, flowering ceasing in the beginning of June. Naturalized. Eurasia.

Barbaraea vulgaris R. Br.

Rare, observed in 6 regions 27 times, mostly as unicates, sometimes as a few specimens. Grows on the tracks as well as on the margins. Eurasia.

Chorispora tenella (Pall.) DC.

Rare, observed in 5 regions 14 times. The pattern of its occurrence is unusual. In the first decade it resembled many other rare Cruciferae in its behavior. It

developed only small colonies, sometimes appearing as unicates (3). Then suddenly in 1971, two huge widely separated colonies developed and flourished through the summer. On the site of the larger colony *C. tenella* had never been seen before, although the tracks concerned had been often visited in the last 5 years. Ripe fruits were abundant. Asia.

CRASSULACEAE

Sedum sarmentosum Bunge

M 2336, 17 May 1964, quite frequent (UMO). *M 2617*, 28 May 1966, 1 colony. *M 3259*, 17 May 1970, few specimens. Asia.

SAXIFRAGACEAE

Philadelphus coronarius L.

M 2330, 10 May 1964 (UMO); *M 2614*, 28 May 1966, ca. 5 shrubs, observed through 1971. Europe.

ROSACEAE

Pyrus communis L.

M 2342, 30 May 1964 (UMO), 1 low shrub, observed through 1969; *M 3155*, 6 Sep. 1969, no trace of the shrub since 1970, although the locality seemed very safe.

Pyrus malus L.

Rare, observed in 4 regions in 7 localities repeatedly. Two specimens were cut down in time. It is less probable that their introductions were caused by railroad traffic, as it is the case in the overwhelming majority of adventives. More likely, they got started from apple cores thrown by the railroadmen or passersby.

Pyrus baccata L.

M 3230, MP at Grand Blvd., 2 May 1970; *M 3402*, 2 Sep. 1970; *M 3494*, 18 Apr. 1971; *M 3564*, 19 June 1971; all from 1 small tree. Determined by K. R. Robertson. Most probably spread, as in other states, from cultivation. Asia.

Fragaria × *ananassa* Duchesne *F. chiloensis* (L.) Ehrh. × *F. virginiana* Duchesne

M 3621, 18 July 1971. *M 3673*, 21 Aug. 1971, 1 small sterile colony each time. In both localities the tracks where the plants occurred had not been used for a long time and in both cases some ornamental shrubs grew directly on the tracks (but were not planted there intentionally).

Potentilla argentea L.

M 3076, Lesperance St. Fr. Yd., 24 May 1969, several colonies. *M 3584*, 26 June 1971, no trace was found in 1970 on the same spot. Determined by F. Markgraf. Eurasia.

Potentilla recta L.

Quite widespread, locally frequent, mostly in colonies which were sometimes of huge size but usually were small, seldom as unicates. Occasionally some flowering recurred in late autumn. Naturalized. Eurasia.

Rubus bifrons Vest

M 3077, 25 May 1969, 1 large and dense colony observed through 1971. Europe.

Rosa multiflora Thunb.

This shrub was first discovered in 1964. In the following years it was still rare, but has been strongly spreading since 1970. Especially along the tracks of Christy Lead (MP), the number of shrubs has obviously increased. No plantings were made here. As it stands now, this rose is quite widespread in St. Louis. The flowers were white, seldom pink. In one case a colony had double flowers in both colors. It is not clear what caused this distinct expansion. The Missouri Department of Conservation fostered the planting of *R. multiflora* along rural fences and roadsides for different purposes, among others, creating wildlife cover. It seems this program has been successful, and naturalization has been achieved. Or it may be that this is a case of endoornithochorous dispersal, similar to the one described by Niemi (1969a) in Finland, where the spread of two *Rosa* species was ascribed to birds, probably crows. Japan.

Rosa rugosa Thunb.

M 2616, 28 May 1966, a dense group of shrubs. The flowers were single. The possibility that the shrubs were planted could not be excluded. They were chopped off in 1970, but some suckers began to develop the next year. Asia.

Prunus persica (L.) Batsch

Widespread, locally scattered, generally as a few or even unicate shrubs. Peaches often develop, but they are of inferior quality. One shrub had pure white flowers. Growth, of course, is possible only on the margins. The source of *P. persica* here must be the same as with the much rarer apple trees—the littered stones of eaten peaches.

Prunus armeniaca L.

M 2987, 22 Sep. 1968, 1 small sterile shrub. Shortly afterwards it was cut down. In 1970 some suckers developed, but in 1971 no trace was found.

LEGUMINOSAE

Cassia occidentalis L.

M 2423, 16 Aug. 1964, 1 specimen (UMO). Tropics.

Trifolium incarnatum L.

M 3238, 9 May 1970, 5 specimens; two were left, but no trace of them was found on 17 June 1970, although no immediate danger seemed to have existed. Europe.

Trifolium pratense L.

Widespread, locally frequent, for the greater part in colonies of moderate size. It prefers the margins and open lots. Astonishingly frequent with *Trifolium*

repens and, to a lesser degree, with *Trifolium hybridum*. Once f. *leucochraceum* Aschers. & Prantl was found: *M 1162*, 30 May 1957, 2 specimens among abundant red ones. Naturalized. Eurasia.

Trifolium repens L.

Widespread, locally frequent but rarer than the previous species. It is also obvious that *T. repens* is rarer on the railroads than in lawns in the city. Mostly in colonies of moderate size. Naturalized. Eurasia.

Trifolium hybridum L.

Quite widespread, locally scattered, in small colonies, but unicates were also found. It prefers margins. Naturalized. Eurasia.

Trifolium campestre Schreb.

M 581, 14 May 1955, 1 small colony; also observed 13 May 1956. *M 598*, 29 May 1955, scattered. MP, Spring Ave. and Vandeventer Ave., 4 June 1956, few specimens. SL-SF, Lindenwood Fr. Yd., 9 June 1956, few specimens. Eurasia.

Trifolium dubium Sibth.

M 608, 29 May 1955, few specimens. *M 597*, 29 May 1955, few specimens. *M 1189*, 2 June 1957, frequent. *M 3258*, 17 May 1970, several large colonies; also observed 20 May 1971. The colonies grew on the margin of the railroad, which received less attention than the tracks. Europe.

Melilotus officinalis (L.) Lam.

Widespread, locally common, for the most part in large, sometimes even in huge, colonies, especially on the margins and open lots. As a rule it begins to flower 2–3 weeks earlier than the next species, *Melilotus albus*, from which it is indistinguishable in sterile stage. In autumn it also stops flowering earlier. Flowering rarely recurs late in the season into November. Naturalized. Once, f. **confertus** O. E. Schulz was found (racemes very short—under 2 cm): *M 3336*, MP elevator, 28 June; *M 3365*, 2 Aug. 1970, the same specimen from which only some branches were taken. Typical *M. officinalis* was frequent in the vicinity. Determined by F. Markgraf. Eurasia.

Melilotus albus Desr.

Widespread, locally common. The distribution is very similar to the previous species, which it frequently accompanies. The only difference is that the late-autumn flowering stragglers are not so rare as in *M. officinalis*. Naturalized. Eurasia.

Medicago sativa L.

Quite widespread, locally scattered, mostly in small colonies. This species is probably becoming rarer. In earlier years the recorded number of localities was considerably higher than in later years. Flowering rarely recurred in late autumn. Eurasia.

Medicago lupulina L.

Widespread, locally frequent, in colonies of different sizes. Besides the typical form, var. *glandulosa* Neilr. was equally frequent. The typical variety seemed,

as a rule, to begin flowering earlier than var. *glandulosa*. Occasionally plants were found in which only the fruits have stalked glands, while their peduncles are covered only with hairs. Once a 4-foliate leaf was discovered on a normal specimen. Naturalized. Eurasia.

Medicago polymorpha L. var. *vulgaris* (Benth.) Shinners

M 1404, 30 May 1958, 1 small colony; *M 1507*, 24 May 1959, 1 specimen. Eurasia.

Coronilla varia L.

M 3672, 21 Aug. 1971; *M 3682*, 29 Sep. 1971, 1 small colony. Eurasia.

Lespedeza cuneata (Dumont) G. Don

M 1697, 4 Sep. 1960, 1 specimen. *M 3681*, 29 Sep. 1971, 1 small colony. Asia.

Lespedeza striata (Thunb.) H. & A.

M 2863, 26 Aug. 1967, 1 dense colony. Asia.

Lespedeza stipulacea Maxim.

Quite widespread, locally scattered in colonies of different sizes, mostly on the margins and open lots. It was especially abundant in the North St. Louis Yard where the St. Louis floodwall is crossed by a roadbed. The banks were sown at least ten years ago by a seed mixture containing 12.8% unhulled Korean *Lespedeza* seeds by weight. The plant is still thriving there. This species and *L. striata* again illustrate a profound distinction in the expansion of both species in St. Louis and Missouri. According to Steyermark (1963), both Lespedezas are quite common in Missouri, but in St. Louis, *L. striata* was found only once, while *L. stipulacea* was by no means a rarity. Naturalized. Asia.

Lespedeza bicolor Turcz.

M 3671, TRRA, Railway Exchange Agency, 21 Aug. 1971, 1 shrub. Determined by D. Isely.

Vicia sativa L. var. *nigra* L. (*V. angustifolia* Reichard)

M 1741, 27 May 1961; *M 1768*, 17 June 1961, the same specimen.

Vicia cracca L.

M 3517, Carrie Ave. Fr. Yd., 8 May 1971; *M 3571*, 20 June 1971, the same large colony. This species was excluded by Steyermark (1963) from the *Flora of Missouri*. The new collections were determined by D. Isely. Eurasia.

Vicia villosa Roth

Rare, observed in 5 regions 20 times, mostly in small colonies or as unicates (7). Only twice were the colonies quite large. Eurasia.

Vicia dasycarpa Ten.

M 95, 29 June 1954, 1 colony. *M 630B*, 5 June 1955, 1 specimen. *M 1151*, 25 May 1957, 1 specimen. *M 3264*, 17 May 1970, 1 small colony, later destroyed. Eurasia.

[*Vicia hirsuta* (L.) S. F. Gray]

This species was quoted in error in the *Flora of Missouri*, p. 940, presumably because of the scrawled label of the writer. The plant in question was *V. dasycarpa* Ten.

Lathyrus hirsutus L.

M 96, 29 May 1954, 1 colony. *M 1506*, 24 May 1959, 1 colony. Eurasia.

Lathyrus latifolius L.

Rare, observed in 5 regions 20 times, but actually the number of localities is much less, only 5. In one case the plant has spread along the N&W trunk line between Riverview Blvd. and Floy Ave. on the unusually wide marginal land of the railroad, creating many isolated colonies quite small in size. It was observed from 1963 through 1971. Flowers were mostly pink, rarely white. In two other localities plants persisted, in one case for 15 years. Nevertheless, there was no expansion. Probably a garden escape in one case, perhaps the result of dumping. Europe.

Pisum sativum L.

Variety *sativum* was found once: *M 2597*, 8 May 1966, 1 small colony. Variety *arvense* (L.) Poir. was also collected one time: *M 561*, 8 May 1955, 1 juvenile specimen without flowers. At several other occasions juvenile *Pisum* specimens were encountered, but no specific determinations were possible.

Phaseolus vulgaris L. var. *humilis* Alef.

M 1228, 22 June 1957, a large colony. *M 1714*, 1 Oct. 1960, 1 specimen. *M 2060*, 21 Oct. 1962, several colonies.

Phaseolus lunatus L. var. *lunonanus* Bailey

M 1304, 11 Aug. 1957, few specimens.

Glycine max (L.) Merr.

Widespread, locally scattered in colonies of varying sizes, including unicates. It does not seem to persist.

LINACEAE

Linum usitatissimum L.

Scattered, observed in 5 regions but in later years evidently becoming rarer. For instance, in 1971 this plant was observed only twice, while in the first year's reports fluctuated between 7 and 11 per season. Frequently found only as unicates, but when found in colonies, they were small. Almost always blue flowered, three times specimens with white corollas were found, once in the midst of a blue-colored colony.

OXALIDACEAE

Oxalis priceae Small subsp. **texana** (Small) Eiten

M 3220, N&W, Mimimica Ave. and Alpha Ave., 25 Apr. 1970, 1 small colony. Determined by D. M. Porter. This species had already been reported once from Missouri under the name *Oxalis recurva* Ell., but it was dropped by Steyermark (1963) in the *Flora of Missouri*. Southeastern U.S.

GERANIACEAE

Erodium cicutarium (L.) L'Hér.

M 1728, 13 May 1961; *M 1742*, 13 June 1961; *M 1769*, 17 June 1961, 3–4 specimens. One fruiting specimen was left, but no trace of this plant was found in following years. Eurasia.

Erodium texanum Gray

M 1762, 30 May 1961, 1 specimen (US). Southwestern U.S.

ZYGOPHYLLACEAE

Tribulus terrestris L.

Widespread, locally frequent in large, sometimes huge, colonies on the tracks as well as on the margins. It flowers from June into November. Naturalized. Eurasia.

SIMAROUBACEAE

Ailanthus altissima (Mill.) Swingle

Widespread, locally scattered. This woody species does not owe its range on the railroads primarily to railroad traffic. This tree is frequent on the streets and in the gardens of St. Louis. The light fruits develop in large numbers and are easily spread by winds. Seedlings appear on many empty lots in the city, and thanks to their rapid growth, they can reach a respectable height in autumn. Rarely may some fruits be brought in by railroad traffic. It is most frequent on margins or on open lots. In some remote corners of yards even tall and fruiting trees are present, and sometimes one may find 1 m and taller stems on rarely used tracks. Naturalized. China.

EUPHORBIACEAE

Croton texensis (Klotzsch) Muell. Arg.

M 1836, 9 Sep. 1961, 1 specimen (US). Southern and western U.S.

Croton lindheimerianus Scheele

M 1965, 2 June 1962, 1 colony. Southwestern U.S.

Ricinus communis L.

M 1268, 7 July 1957, 1 small colony, observed through 1961, it then disappeared, although the locality was very safe. TRRA, Bremen Fr. Yd., 29 Sep. 1957, 1 specimen. SL-SF, Lindenwood Fr. Yd., 16 Sep. 1962 and 10 Oct. 1963, few specimens. N&W, St. Louis Ave. Fr. Yd., 4 July 1963, 1 colony; it was later chopped down but flowered again on 3 Nov. 1963. *M 2490*, 5 July 1965, 2 specimens. Africa.

Chamaesyce prostrata (Ait.) Small (*Euphorbia prostrata* Ait.)

M 2417, 15 Aug. 1963 (UMO), observed through 1968, 1 colony. *M 2751*, 12 Oct. 1966, frequent. *M* 2887, 7 Oct. 1967, 1 colony. Tropical America.

ANACARDIACEAE

Rhus typhina L. f. *dissecta* Rehder

M 930, 9 June 1956, 1 shrub, also 27 June 1964, later destroyed. Surely a garden escape—the same ornamental was observed in the neighboring gardens. Northeastern U.S.

CELASTRACEAE

Euonymus fortunei (Turcz.) Hand.-Maz. var. **radicans** Rehder

M 3142, SL-SF at Kingshighway, 30 Aug. 1969, few specimens. Determined by K. R. Robertson. Surely a garden escape. Often cultivated as a ground cover in St. Louis, although there were no gardens in the vicinity. No trace of it was seen the next year. Asia.

BALSAMINACEAE

Impatiens balsamina L.

M 3388, 25 Aug. 1970, 1 specimen. A garden escape. Asia.

VITACEAE

Parthenocissus tricuspidata (Sieb. & Zucc.) Planch.

Rare, met in 2 regions in 6 localities. First seen 1964 in the South Ranken Fr. Yd. (TRRA), on even ground next to a track. All other localities were on the walls of buildings along the tracks. Some persistence was noted, the longest being 7 years. It is probably in most cases a garden escape from the neighboring gardens. Asia.

Vitis labruscana Bailey

M 1120, 12 Oct. 1956, observed through 1963, laying directly on the ground without any support, few specimens. An escaped cultigen.

MALVACEAE

Malva sylvestris L.

M 3689, 6 Oct. 1971; *M* 3733, 20 Nov. 1971, the same 3 specimens. Eurasia.

Malva neglecta Wallr.

M 69, 23 May 1954, 1 small colony. Eurasia.

Malva rotundifolia L. (*M. pusilla* Sm.)

Rare, observed in 3 regions 6 times, only once as a small colony but 4 times as unicates. Eurasia.

Alcea rosea L. (*Althaea rosea* (L.) Cav.)

Widespread, locally rare. Surely a garden escape—once even found with double flowers. The color of the flowers was very varied, frequently white and pink, more rarely red and yellow. Sometimes different colors were represented in the

same colony. Mostly on open lots and margins; unicates were not rare. This plant has proven to be persistent in some places. Eurasia.

Anoda cristata (L.) Schlecht.

M 3062, 26 Oct. 1968, 1 specimen. Texas to Arizona.

Sida spinosa L.

Widespread, locally scattered. *Sida spinosa* was very frequently accompanied by the next species, *Abutilon theophrasti*. This association greatly facilitated the detection of this inconspicuous species. The colonies of *S. spinosa* were usually small, although unicates were also found. Tropics.

Abutilon theophrasti Medic.

Widespread, locally scattered in colonies of different sizes, several of them were huge—especially on freshly disturbed soil as after bulldozing. Unicates were quite rare. Naturalized. Eurasia.

Hibiscus syriacus L.

M 1370, 14 Sep. 1957. *M 2712*, 27 Aug. 1966, 1 low shrub each time. Surely a garden escape. Asia.

Hibiscus trionum L.

Rare, observed in 3 regions 31 times. In this species unicates were prevalent (22); in the remaining cases only small colonies were found. It was primarily found on the tracks. Eurasia.

Gossypium hirsutum L.

M 1690, 3 Sep. 1960 (US), 3 specimens. *M 2024*, 18 Aug. 1962, 1 colony. *M 2726*, 18 Sep. 1966, observed through 1968, 1 colony. MKT, Baden Fr. Yd., 2 Sep. 1967, 2 isolated specimens. Only once were flowering specimens met; therefore one is inclined to accept repeated introductions. Determined by P. A. Fryxell and D. M. Bates, although originally published by Steyermark (1963) as *G. herbaceum* L.

[*Gossypium herbaceum* L.]

Cited in the *Flora of Missouri*, p. 1652, it is *G. hirsutum* L. according to P. A. Fryxell and D. M. Bates.

STERCULIACEAE

Melochia corchorifolia L.

M 2880, Tyler St. Fr. Yd., 9 Sep. 1967, 3 specimens. Determined by L. H. Shinners. Paleotropics.

GUTTIFERAE

Hypericum perforatum L.

Rare, observed in 4 regions 8 times, in small, partly persistent colonies, but also as unicates (2). Eurasia.

TAMARICACEAE

Tamarix gallica L.

M 765, 10 Sep. 1955, 2 shrubs, later destroyed. Europe.

VIOLACEAE

Viola tricolor L.

M 875, 5 May 1956, 1 small colony. It was probably introduced by the dumping of garden refuse. Eurasia.

Viola kitaibeliana R. & S. var. *rafinesquii* (Greene) Fern.

Quite widespread, but observed only 18 times. One circumstance must be considered: It is an especially short-lived plant and disappears entirely towards the end of May. It always occurs in colonies of mostly moderate size. Opinions about the origin of this plant differ vastly. Some place its origin in southeastern Europe and northern Africa; others believe it to be a native, quite widespread in the United States. The last view is supported by Gleason (1968) among others. But even accepting the latter opinion, the question remains whether Missouri should be included in the primary range of this species. The species does seem to be expanding its range. Steyermark (1963) also noted that it is "apparently spreading (in Missouri) northward." My impression is, that *V. kitaibeliana* is not so rare now on the railroads as in previous years.

ONAGRACEAE

Oenothera kunthiana (Spach) Munz

M 1392, 20 Oct. 1957; thereafter collected several times more, the last time observed, 1962. Texas.

Gaura sinuata Nutt. ex Ser.

M 2760, 12 Oct. 1966, 1 dense colony. The plants were found on an old car cleanout track, the use of which was discontinued several years before their discovery. The place was visited regularly several times each year. As another, also conspicuous plant (*Physalis acutifolia*), was found nearby, it is difficult to assume that both plants were constantly overlooked. The wide separation of former cleanout tracks and the yard itself argues against the possibility of these being recent introductions from the yard. This is most likely a case of seed dormancy, a phenomenon well known to European adventive botanists. Texas and Oklahoma.

ARALIACEAE

Hedera helix L.

M 764, 10 Sep. 1955, 1 large colony, observed through 1964 and then destroyed. Probably a garden escape. Eurasia.

UMBELLIFERAE

Anthriscus scandicina (Weber) Mansf.

M 887, 13 May 1956; *M 960*, 17 June 1956, few specimens; *M 1150*, 25 May 1957, 1 colony. Although the locality was secluded and unthreatened, the plant did not appear in 1958 or thereafter. Eurasia.

Torilis arvensis (Huds.) Link

Widespread, locally scattered, always in colonies. It was long mistaken for *T. japonica* (Houtt.) DC. until M. E. Mathias redetermined this material. Howell (1962) had also pointed out this confusion and noted that *T. japonica* is quite rare. In spite of careful examination of each *Torilis* colony in the years 1970 and 1971, *T. japonica* could not be found. Naturalized. Eurasia.

Torilis nodosa (L.) Gaertn.

M 1403, 30 May 1958, 1 small colony. Eurasia.

Coriandrum sativum L.

M 1248, 30 June 1957, 4 specimens. *M 1975*, 17 June 1962, a large colony, also observed in 1963. Eurasia.

Conium maculatum L.

Rare, observed in 4 regions in 6 localities. In Region 4 it persisted for 8 years and created a huge colony. In other cases the colonies were small and passing; unicates were also found (2). Eurasia.

Apium graveolens L.

M 1349, 7 Sep. 1957, 2 specimens. *M 2558*, 26 Sep. 1965, 1 specimen. In both cases the plants were sterile.

Ammi majus L.

M 1539, 4 July 1959, 2 specimens. Eurasia.

Anethum graveolens L.

M 939, 16 June 1956, 1 specimen. MP, N of Biddle St., 7 July 1957, 1 specimen. N&W, St. Louis Ave. Fr. Yd., 17 June 1962, 3 specimens. *M 3105*, 21 June 1969, 1 specimen.

Pastinaca sativa L.

Quite widespread, locally frequent, often in large colonies, especially on the margins. It was probably not an escaped cultigen, but the weedy wild form. Naturalized. Europe.

Daucus carota L.

Widespread, locally scattered, mostly in small colonies. In late autumn (October–November) a second flowering could often be observed, but the plants were mostly unicates then. It was almost certainly the weedy wild form, not the escaped cultigen. Naturalized. Eurasia.

PRIMULACEAE

Anagallis arvensis L.

Rare, observed in 4 regions 7 times, once two years in a row as small colonies or as unicates (2). Only the typical form with scarlet flowers was found. Eurasia.

LOGANIACEAE

Buddleia davidii Franch.

M 3622, Union Station, not planted, 18 July 1971, 1 shrub, later destroyed. Determined by E. Norman. China.

ASCLEPIADACEAE

Asclepias subverticillata (Gray) Vail

M 2000, 28 July 1962, a large colony. The colony flourished until 1970, in spite of constant use of weed killers and at least one devastating fire which swept over the ground. Southern and western U.S.

CONVOLVULACEAE

Ipomoea coccinea L.

Rare, observed in 4 regions 18 times, in colonies of different sizes, always on margins, climbing on bushes and fences. It was subsequently found on several sites, apparently on the same spot, but skipping many years. Overlooking this quite conspicuous annual plant continuously is inconceivable; therefore, reintroductions or seed dormancy may be involved. Tropical America.

Ipomoea hederacea (L.) Jacq.

Widespread, locally scattered, always in colonies of different sizes, commonly found on the tracks and around grain elevators. Climbing was very rarely observed. Naturalized. Variety *integriuscula* Gray was found in 4 regions 11 times. Tropical America.

Ipomoea purpurea (L.) Roth

Widespread, locally scattered, in colonies of different sizes on margins and open lots. Mostly climbing, but procumbent specimens were occasionally seen. The prevalent colors of the corollas were purple and red, but white corollas were also observed. *Ipomoea purpurea* is probably at least partly a garden escape, as it is common in city gardens. That is less conceivable in the case of the previous species, *I. hederacea*, which seems much less suitable as an ornamental, although Bailey (1960) cited it in his *Manual of Cultivated Plants*. Very rare was var. *diversifolia* (Lindl.) O'Donell: *M 811*, 25 Sep. 1955, a small climbing colony, observed through 1971. Tropical America.

Ipomoea cairica (L.) House

M 1711, 1 Oct. 1960, few specimens (US). Africa.

Jacquemontia tamnifolia (L.) Griseb.

M 3188, Lesperance St. Fr. Yd., (MP) 5 Oct. 1969, 1 specimen. *M 3408*, Carr. St. Fr. Yd., 6 Sep. 1970, 2 specimens. Determined by K. R. Robertson. Southeastern U.S.

Convolvulus pellitus Ledeb. f. *anestius* Fern.

M 601, 29 May 1955, 1 colony. *M 2463*, 22 May 1965, 1 small colony. Probably a garden escape. China.

Convolvulus arvensis L.

Widespread, locally common, mostly in large colonies. It could be found everywhere. Naturalized. Eurasia.

Cuscuta indecora Choisy var. *neuropetala* (Engelm.) Hitchc.

M 973, 30 June 1956, 1 large colony; *M 1462*, 9 Aug. 1958, several colonies. The principal range of this species seems to be in the southern United States, but it also has several extensions to the northern states, among others, Illinois and Minnesota. Therefore the plant could be native in Missouri also, but the locality was directly on the tracks, where other adventives were found. The hosts were the common *Convolvulus arvensis* and a completely dried crucifier, probably *Erysimum repandum*.

BORAGINACEAE

Heliotropium indicum L.

M 2171, 17 Aug. 1963, 1 colony. Asia.

Echium vulgare L.

M 643, 18 June 1955, 1 specimen. Eurasia.

Lithospermum arvense L.

Widespread, locally scattered, mostly in small colonies. Being a vernal plant, it disappears in the first half of June. This was the first adventive ever observed in this study, 17 April 1954. Eurasia.

Amsinckia lycopsoides Lehm.

M 893, 30 May 1956, 1 colony. *M 959*, 17 June 1956. *M 1772*, 17 June 1961 (US). *M 2083*, 30 May 1963, in the last 3 localities, 1 specimen each time. Western U.S.

Amsinckia hispida (R. & P.) Johnston (*A. micrantha* Suksd.; *A. retrorsa* Suksd.)

M 2363, 20 June 1964, 1 specimen. *M 2368*, 21 June 1964, 5 specimens. Western U.S.

Amsinckia tesselata Gray

M 44, 23 May 1954, 1 small colony. *M 2790*, 27 May 1967, 1 specimen; only parts were taken, but there was no trace of the plant the next year. Western U.S.

Lappula echinata Gilib.

Rare, observed in 4 regions 21 times, especially common in Region 1. Prevalently found as unicates (17) but in other cases, where there were several specimens,

they were spread widely over the yards, so that it was impossible to speak of colonies. This distribution pattern was quite striking. The nutlets, four in each flower, are provided with prickles and one might expect several nutlets to be transferred simultaneously. Apparently this does not happen. Eurasia.

Lappula redowskii (Hornem.) Greene var. **redowskii**

M 2787, 27 May 1967; *M 3530*, 16 May 1971, 1 specimen each time. Determined by J. L. Gentry, Jr. Western U.S.

VERBENACEAE

Verbena brasiliensis Vell.

M 3439, 20 Sep. 1970, 3 specimens; *M 3466*, 29 Oct. 1970; although one specimen was left, no trace of this plant was found the next year. Determined by H. N. Moldenke. South America.

Verbena halei Small

M 1256, 4 July 1957, 1 specimen. *M 1423*, 28 June 1958, 2 specimens; *M 1607*, 22 May 1960, 4 specimens, only two were taken, but no trace of the plant was found the next year. All specimens in the Moldenke Herbarium. Southern U.S.

LABIATAE

Nepeta cataria L.

Rare, observed in 4 regions 24 times, in the majority of cases as unicates (15) or as small colonies. One colony was observed in two succeeding years, but no persistence, let alone naturalization, had been achieved. Eurasia.

Glechoma hederacea L. var. *micrantha* Moricand

Rare, observed in 4 regions in 7 localities, in two constantly over 17 and 12 years. It always grew in colonies, never on the tracks. The long-persisting colonies grow in deep shade. Eurasia.

Dracocephalum parviflorum Nutt.

Rare, observed in 2 regions 11 times, typically as unicates, rarely as 2 or 3 specimens. It is widely spread in the U.S., especially in the northern states, and Gleason (1968) also cites Missouri. On the other hand, Steyermark (1963) explicitly mentions it as introduced here.

Leonurus cardiaca L.

Quite widespread, locally scattered, always in colonies of different sizes. It was persistent in quite a few localities—in one even for 17 years. In some localities there seems to be some expansion of the sites. Naturalized. Eurasia.

Galeopsis tetrahit L.

M 934, 16 June 1956. *M 978*, 30 June 1956. *M 992*, 1 July 1956. In all localities one specimen at a time. Eurasia (Fernald, 1950) or Europe (Komarov, 1933–1964).

Lamium amplexicaule L.

Widespread, locally common, always in colonies of different sizes on the margins and open lots, as well as on the tracks. Besides the typical form with well-developed corollas, f. *clandestinum* (Reichenb.) G. Beck with cleistogamous flowers was equally frequent. Flowering started in March and continued into June, when the plant disappeared. In October, very rarely in the last half of September, flowering recurred on freshly grown specimens, but then they were rare and almost always f. *clandestinum*. Naturalized. Eurasia.

Lamium purpureum L.

Rare, observed in 4 regions in 12 localities, in colonies of very varied sizes. The impression is that this species is, to some extent, failing here, though it must be added that 5 localities were discovered in the last two years of this study. In contrast to the previous species, no late autumn flowering was ever noticed. Eurasia.

Mentha spicata L.

M 3652, 1 Aug. 1971, 1 colony. Europe.

Mentha × *gentilis* L. (*M. arvensis* L. × *M. spicata* L.)

M 301, 8 Aug. 1954, observed through 1971. *M 813*, 25 Sep. 1955, observed through 1971. *M 1103*, 22 Sep. 1956, observed through 1964. *M 3363*, 2 Aug. 1970. *M 3446*, 18 Oct. 1971. In all places, the plants grew in colonies, and showed remarkable persistence. R. M. Harley (pers. comm.), who determined the *Mentha* material, stated that these "plants are close to the form of the hybrid, which has been known as *M. cardiaca* (S. F. Gray) Baker, a widely cultivated plant." Europe.

Perilla frutescens (L.) Britt.

M 1088, 15 Sep. 1956, 1 specimen. *M 2034*, 16 Sep. 1962, 1 colony, observed through 1964. *M 3199*, 21 Oct. 1969, 1 large colony, also observed 25 Oct. 1970, 3 specimens. *M 3480*, 7 Nov. 1970, 1 specimen. This is probably, at least in part, a garden escape. Asia.

Ocimum basilicum L.

M 1333, 1 Sep. 1957, 1 specimen. It is most probably a garden escape. Asia.

SOLANACEAE

Solanum tuberosum L.

Rare, observed in 3 regions 20 times, although only sprouting tubers were observed. Flowering was never observed, although very immature flower buds were seen twice. It was especially frequent along the unloading platforms of the St. Louis Produce Market.

Solanum sarachoides Sendtner

M 1436, 4 July 1958, 2 specimens. South America.

[*Solanum villosum* Mill.]

Cited in the *Flora of Missouri*, p. 1312, it is, according to W. G. D'Arcy, in one case *Solanum sarachoides*; in the other the specimens are too juvenile for certain determination.

Solanum rostratum Dunal

Scattered, observed in 6 regions, mostly in colonies of modest size, but also as unicates. It was often found on the tracks. Although the plant has been labeled an aggressive weed, it has not been able to gain a firm footing in St. Louis's railroads. On the contrary, it has become decidedly rarer during the years of this study. Western U.S.

Lycopersicum esculentum Mill.

Quite widespread, locally scattered, mostly in colonies of different sizes, but also as unicates. The development of the fruits was almost always retarded—only once were reddish tomatoes of considerable size. It was probably mostly spread by the movement of produce. Since it was spread quite evenly over all regions, it was quite likely that the throwing away of good remains was also important in its dissemination, and it probably also becomes attached to shoes and is subsequently spread about. The seeds of tomato are very enduring according to my experience. Tomato can even be found growing on sludge after sewage treatment, including chlorination. Direct escape from gardens is probably less important.

Physalis viscosa L. var. *cinerascens* (Dunal) Waterfall

M 2486, 5 July 1965, 1 specimen. Southern and southwestern U.S.

Physalis acutifolia (Miers) Sandw. (*P. wrightii* Gray)

M 2759, 12 Oct. 1966, 1 specimen. Southern and southwestern U.S.

Lycium halimifolium Mill.

Widespread, locally scattered, always in large, dense thickets, on margins and open lots. Observed in several locations through all years. Naturalized. Europe.

Datura stramonium L.

Quite widespread, locally scattered, mostly in colonies of different sizes, although unicates were also found. Observed in several localities for many years. Naturalized. Its origin is sometimes said to be Asia, sometimes South America. Very rare was var. *tatula* (L.) Torr.: *M* 322, 8 Aug. 1954, 1 specimen. Often specimens were seen in which the stems and corollas had some tint of lavender or violet which is intermediate between true var. *stramonium* and *tatula*. Curiously, green stems and pure white corollas typical of var. *stramonium* were mostly seen in low specimens. Eurasia.

Datura innoxia Mill.

Rare, observed in 4 regions in 8 localities, in small colonies or as unicates (3). In two localities repeatedly seen for 2 and 3 years. Tropical America.

Petunia axillaris (Lam.) B. S. P.

M & Anderson 707, 6 Aug. 1955, 1 specimen. A garden escape, although there were no gardens in the vicinity. South America.

Petunia × *atkinsiana* D. Don (*P. violacea* Lindl. × *P. axillaris* (Lam.) B. S. P.)
Rare, observed in 5 regions 15 times, mostly in small colonies, only once was a very large colony discovered on a big open lot, which had previously been bulldozed for industrial development. For this ergasiophyte Steyermark (1963), as well other leading floras, use the name of one of the parents—*Petunia violacea* Lindl. E. Anderson emphatically opposed this practice because of the hybrid status of this taxon. F. G. Meyer, who determined one collection, called this plant *Petunia* × *atkinsiana*. South America.

SCROPHULARIACEAE

Verbascum thapsus L.
Widespread, locally frequent, in colonies of very different sizes, some of them huge, on margins and open lots, as well as on the tracks, but in the last case the tall plant was stunted by passing freight trains. In a few cases unicates were seen. Naturalized. Eurasia.

Verbascum blattaria L.
Quite widespread, locally scattered, in colonies of modest size or seldom as unicates. Both corolla color forms were encountered—f. *blattaria* (yellow) and f. *erubescens* Brugger (white)—occasionally in the same colony. As elsewhere, f. *erubescens* was more common. Naturalized, although no persistence was noted. Eurasia.

Kickxia elatine (L.) Dumort.
Rare, observed in 5 regions in 8 localities. It was a true ephemerophyte in 6 localities, but one colony, discovered in 1955, grew through 1970, after which it was destroyed by lubricants and paint. Another colony persisted for 5 years. Europe.

Linaria vulgaris Hill
Rare, observed in 4 regions in 6 localities, with one exception in colonies of different sizes. Remarkable was the tendency to persist for prolonged periods of time. One colony, under observation for 9 years, still flourished, but two other colonies which persisted for 8 years vanished without obvious causes. This is a case which shows why one should be exceedingly reserved in predicting naturalization for a species. Europe.

Antirrhinum majus L.
M 1050, 25 Aug. 1956, 1 colony. The plant must have been a garden escape through dumping of garden refuse. The color of the corollas in single specimens was widely different, including greenish yellow, which never appears in wild plants. Europe.

Chaenorrhinum minus (L.) Lange
Observed in 4 regions. It was first discovered in 1955, and 4 more localities were discovered through 1969. In all these only 1–5 specimens were observed. Suddenly since 1970, 5 localities were discovered with the plants growing in large,

sometimes even huge, colonies. What evoked this "explosion" is not known. *Chaenorrhinum minus* was a very rare plant through 1969, but must now be designated as scattered or frequent. Europe.

Paulownia tomentosa (Thunb.) Steud.

M 2347, 31 May 1964, 6 specimens. These shrubs, growing close to the right-of-way of the railroad produced suckers that managed to reach the nearest, rarely used track and began to grow between the rails. These suckers were later destroyed, but the shrubs themselves, although several times heavily damaged, survived through 1971. Asia.

Veronica arvensis L.

Widespread, locally common, often in huge dense colonies on open lots and margins, as well as on the tracks. It is a typical vernal plant and ceased to flower in the first half of June. Only once were fresh, but sterile, specimens found in November. Naturalized. Eurasia.

Veronica polita Fries

M 3224, 25 Apr. 1970, 1 small colony. Eurasia.

BIGNONIACEAE

Catalpa bignonioides Walt.

M 1623, 4 June 1960, 3 flowering trees. It is very likely that *C. bignonioides* is not at all so rare as the sole collection would indicate. Catalpas are not at all rare on the railroads, especially on some unused tracks. Some could not be determined with certainty and others were probably the native *C. speciosa* Warder. They are usually very low shrubs, sometimes even seedlings. Southeastern U.S. (from Georgia to Mississippi).

PEDALIACEAE

Sesamum orientale L. (*S. indicum* L.)

M 3148, 1 Sep.; *M 3181*, 4 Oct. 1969, 4 specimens from the same colony. Africa.

PLANTAGINACEAE

Plantago major L.

M 743, 4 Sep. 1955, 1 small colony. *M 2544*, 19 Sep. 1965, 1 specimen. *M 2650*, 25 June 1966, few specimens. *M 2954*, 4 July 1968, 1 small colony. *M 3658*, 7 Aug. 1971, 1 colony. It was possibly often overlooked since the very similar looking native *P. rugelii* Dcne. frequently accompanied this species. However, according to Steyermark (1963), *P. major* is rare elsewhere in Missouri also. Eurasia.

Plantago lanceolata L.

Widespread, locally frequent. It was an especially gregarious species—never was a unicate located. The size of colonies was quite variable, mostly of

moderate size. Occasionally a monstrosity with compound and lobate spikes was encountered. Naturalized. Eurasia.

Plantago wrightiana Dcne.

M 1779, 18 June 1961, 1 colony (US), observed through 1964 and then destroyed. *M 2376*, 28 June 1964 (UMO), 3 specimens. *M 2646*, 19 June 1966, 1 specimen (DAO). Texas and Arizona.

CAPRIFOLIACEAE

Lonicera xylosteum L.

M 3528, 15 May 1971; *M 3568*, 19 June 1971; *M 3605*, 10 July 1971; *M 3675*, 22 Sep. 1971, all from the same shrub. Probably a garden escape. Eurasia.

Lonicera morrowii Gray

M 2124, 30 June 1963, 1 shrub, observed through 1971. *M 3561*, 6 June 1971, 1 shrub. Probably a garden escape. Eurasia.

Lonicera japonica Thunb.

Quite widespread, locally scattered, observed in 12 localities, some persistent for a long time. *Lonicera japonica* grew on margins, especially in proximity to other shrubs on which it begins to twine. Another preferred site was on border fences. Once a colony was discovered growing without any support. In St. Louis it can hardly be described as a pernicious weed as was done by Fernald (1950). The colonies were modest in size and, where persistent, showed no tendency to expand. Naturalized. Asia.

DIPSACACEAE

Dipsacus sylvestris Huds.

M 347, 14 Aug. 1954, a huge colony, persisting through 1971, but not spreading very much. *M 2012*, 4 Aug. 1962, but first observed 8 May 1955, 1 small colony, observed through 1970 and then destroyed, also very inactive in spreading. Naturalized. Eurasia.

CUCURBITACEAE

Cucurbita pepo L. var. *ovifera* (L.) Alef.

Rare, observed in 2 regions 6 times. Widely isolated specimens were repeatedly observed in the same yard; it seemed improper to speak in such cases of only one locality. The plants grew mostly as unicates, sometimes reaching huge sizes. In 4 localities undeniable dumping had taken place.

Cucumis melo L.

Rare, observed in 3 regions 9 times, as unicates (5) or as small colonies, with some preference for tracks (6). For the most part no obvious signs of dumping (in contrast with the previous species) were obvious. Several times noticeable fruits were beginning to develop.

Cucumis sativus L.

M 1847, 9 Sep. 1961, 1 specimen.

Citrullus lanatus (Thunb.) Mansf. (*C. vulgaris* Schrad.)

This was the most common escape in the gourd family. Quite widespread, locally rare, observed 35 times, mostly in small colonies, but also as unicates (16). No special site preference was obvious, nor did its appearance appear to be connected with dumping.

Lagenaria siceraria (Molina) Standley (*L. vulgaris* Ser.)

M 1055, 2 Sep. 1956. *M 1476*, 31 Aug. 1958. *M 3630*, 22 July 1971; *M 3717*, 1 Nov. 1971, everywhere as small colonies.

CAMPANULACEAE

Campanula rapunculoides L.

M 3322, 23 June 1970; *M 3691*, 6 Oct. 1971; *M 3718*, 1 Nov. 1971, all one colony. It is sometimes considered a garden escape by American botanists, and it was found in a region where garden escapes were especially frequent. However, many other *Campanula* species are much showier and more desirable as ornamentals. Furthermore, Hegi (1908–1931) considered it only a weed and a ruderal plant in Europe. Most likely that is the case here also. Europe.

COMPOSITAE

Eupatorium capillifolium (Lam.) Small

Rare, observed in 2 regions in 6 localities, mostly as unicates, only once as 2 specimens. It flowered very late in October. Chiefly in the Atlantic and Gulf Coast U.S. (from New Jersey to Texas).

Grindelia squarrosa (Pursh) Dunal var. *serrulata* (Rydb.) Steyerm.

M & Anderson 712, 6 Aug. 1955, few specimens. Western U.S.

Gutierrezia texana (DC.) T. & G.

M 1715, 1 Oct. 1960, 1 specimen. Southwestern U.S.

Franseria discolor Nutt.

M 439, 19 Aug. 1954, 1 large colony, which persisted for many years, in spite of continual spraying with weed killers. Last observed in 1968. *M* 738, 28 Aug. 1955, 2 specimens. Western U.S. and Illinois. Therefore, the possibility that *Franseria discolor* is in reality a native plant cannot be ignored, but since it grew with many typical adventives, it is more likely that it belongs to the latter category.

Ratibida tagetes (James) Barnhart

M 1865, 16 Sep. 1961, 1 huge specimen (US); *M 2419*, 15 Aug. 1964, 1 specimen (UMO). Western and southwestern U.S.

Verbesina encelioides (Cav.) B. & H. var. *exauriculata* Robins. & Greenm.

Observed in 4 regions. It was very irregularly distributed, ranging from common

in some areas to rare in others. It grew as unicates or in huge colonies that persisted for many years. Profuse flowering started in mid-May and continued without intermission into November. Naturalized. Western and southern U.S.

[*Thelesperma ambiguum* Gray]

Cited in the *Flora of Missouri*, p. 1653, it is actually *T. trifidum* (Poir.) Britt. according to a determination at the Smithsonian. This latter species is native to Missouri.

Coreopsis cardaminefolia (DC.) T. & G.

M 1829, 20 Aug. 1961, 1 specimen (US). Western and southern U.S.

Bidens coronata (L.) Britt.

M 3706, Luther Fr. Yd., 17 Oct. 1971, 3 specimens. Determined by R. P. Wunderlin. The plants grew on the edge of a newly established parking lot, bordering on a preexisting wet depression where some plants of wet habitats grew. *Bidens coronata* is a plant of wet habitats, a group of plants which seldom produce adventives, so it is possibly a native element, until now overlooked. Steyermark (1963) grouped it with those species that he thought most likely to extend into Missouri from Illinois. According to Jones (1955), it grows on moist ground throughout Illinois, including St. Clair County which is just opposite the city of St. Louis. Widely spread in the U.S., mostly in the eastern and northern states.

Bidens pilosa L. var. **radiata** Schz.-Bip.

M 3046, Baden Fr. Yd., 24 Oct. 1968, 1 large specimen. Determined by R. D. Weedon. Although only a few branches were taken, it did not appear the next year. Tropical America.

Cosmos bipinnatus Cav.

M 1471, 30 Aug. 1958, 1 specimen. A garden escape. Mexico.

Cosmos parviflorus (Jacq.) Pers.

M 2285, Carrie Ave. Fr. Yd., 20 Oct. 1963, 1 specimen. Determined by T. E. Melchert. Western and southern U.S.

Galinsoga ciliata (Raf.) Blake

M 1617, 30 May 1960, 1 specimen. *M 1958*, 30 May 1962, 1 specimen; *M 2812*, 18 June 1967. RI, Carrie Ave. Fr. Yd., 7 Oct. 1967, 4 specimens. *M 2556*, 26 Sep. 1965, observed through 1968, always in colonies. Tropical America.

Gaillardia pulchella Foug.

M 1003, 8 July 1956, 1 specimen. *M 3390*, 25 Aug. 1970, 1 specimen. Probably a garden escape. The first one was far removed from all gardens. Western and southern U.S.

Tagetes patula L.

M 1461, 27 July 1958, 2 specimens. *M 2507*, 7 Aug. 1965, 1 specimen. Probably a garden escape. Mexico.

Achillea millefolium L.

Widespread, locally scattered, mostly in colonies of modest size, especially on margins. Naturalized. Eurasia.

Anthemis cotula L.

Rare, observed in 5 regions 31 times, occasionally quite a few isolated specimens were spread over a whole yard; however, normally it appeared in colonies of modest size, or seldom as unicates (3). A predilection for tracks was evident. Europe.

Anthemis arvensis L.

Rare, observed in 3 regions 8 times, usually in small colonies, thrice unicates, once in a mixture with *Anthemis cotula*. Eurasia.

Matricaria chamomilla L.

Rare, observed in 4 regions 20 times, mostly in small colonies, sometimes as unicates (6). Eurasia.

Matricaria matricarioides (Less.) Porter

Rare, observed in 3 regions 10 times, mostly small colonies, twice as unicates. Only once did a large colony develop, which persisted for 3 years. *Matricaria matricarioides*, which originates in northeastern Asia or in northwestern America, or according to others, in both, is a real puzzle to me. The reports about the phenomenal spread of this species in the last 100 years are innumerable. As Hegi (1908–1931) emphasized, it spread out especially along the railroads. In 1931 it was present in almost every railroad station in Germany. Moreover, Jones & Fuller (1955) reported that this adventive weed was apparently so well established in St. Louis by 1825 that G. Engelmann mistook it for a native plant. In Missouri it is scattered throughout the state and reported from 20 countries (Steyermark, 1963). It was not known in Chicago prior to 1930, but it has increased tremendously in the entire Chicago region in recent years (Swink, 1969). Therefore its rarity on St. Louis railroads is astonishing.

Chrysanthemum leucanthemum L.

Quite widespread, locally rare, observed 40 times, in half of them as unicates, in the other, almost always as small colonies. Fernald (1950) described it as a pernicious but beautiful weed. Bailey (1960) noted that it is probably not regularly cultivated, although it perhaps appears in gardens. In St. Louis it is tolerated in many gardens and spared during grass mowing. It appeared primarily along the N&W trunk line (Region 7), where an abundance of garden escapes was observed during the survey due to widespread dumping of garden refuse. Elsewhere, its introduction as a weed was more probable. Naturalized. Eurasia.

Tanacetum vulgare L.

M 3038, 21 Oct. 1968, 1 miserable specimen. Eurasia.

Artemisia biennis Willd.

M 932, 16 June 1956; *M 1012*, 14 July 1956; *M 1258*, 7 July 1957, 1–4 specimens. *M 1414*, 7 June 1958, ca. 12 specimens. TRRA, Harlem Fr. Yd., 28 June 1958, 1 specimen and 13 June 1959, 1 colony. Supposedly northwestern U.S.

Artemisia vulgaris L.

Rare, observed in 3 regions in 6 localities, always in colonies of different sizes, mostly repeatedly, with the longest observation time 4 years. It was first found in 1956 and Steyermark (1963) in his *Flora of Missouri* subdivided it, probably unnecessarily since all plants came from a very small area, into three varieties—var. *vulgaris*, var. *glabra* Ledeb., and var. *latiloba* Ledeb.

Artemisia absinthium L.

M 1656, 25 June 1960. *M 2777*, 9 Apr. 1967, in each case a single rosette which was later destroyed. *M 1695*, 3 Sep. 1960, one strong rosette, growing on a track with quite heavy traffic. It was later (1962 or early 1963) transplanted to someone's garden. Eurasia.

Senecio vulgaris L.

M 1428, 28 June 1958. *M 1645*, 19 June 1960. *M 2092*, 30 May 1963, all as unicates. Eurasia.

Senecio ampullaceus Hook.

M 1735, 21 May 1961, 6 specimens (US). Two were left, but no trace of the plant was found the next year. Texas.

Arctium minus (Hill) Bernh.

Quite widespread, locally scattered, in colonies of different sizes, almost always on margins and open lots. In several localities it was observed for many years, but at others it disappeared. Naturalized. Europe.

Carduus nutans L.

Quite widespread, locally scattered. There is no doubt that it has managed to expand its range in St. Louis greatly. From 1954 to 1956 only 3 occurrences as unicates or as a few specimens were recorded. In contrast, in 1971, 24 colonies were counted, many of them huge and having persisted for many years. It also appears now in the city on vacant lots. Naturalized. Eurasia.

Cirsium vulgare (Savi) Ten. (*C. lanceolatum* (L.) Hill)

Quite widespread, locally scattered, in small colonies or as unicates, margins and open lots are preferred. It may be confused with some of the native species and may sometimes have been misidentified. Naturalized. Eurasia.

Cirsium arvense (L.) Scop.

Although Fernald (1950) has called it a ubiquitous weed of cultivation and waste ground, *C. arvense* is a rarity here. It was observed in 4 regions 31 times, mostly in colonies of moderate size and was frequently encountered repeatedly. Some colonies were found to be sterile, even in the autumn. Nevertheless, it

seems that naturalization is achieved. The longest observation time of a colony was 8 years. Eurasia.

Cirsium texanum Buckley

All in TRRA, South Ranken Yd., *M 2478*, *M 2480*, 27 June 1965, 2 isolated specimens; *M 2663*, 4 July 1966, 1 specimen. Determined by L. H. Shinners and G. B. Ownbey. Texas and Oklahoma.

Centaurea solstitialis L.

M 970, 24 June 1956. *M 1425*, 28 June 1958. *M 1877*, 30 Sep. 1961, in all cases 1 specimen. Eurasia.

Centaurea diffusa Lam.

M 1641, 19 June 1960, 2 specimens. The plant grew through 1970. The fluctuation in the number of plants was remarkable. In some years only 2 specimens could be counted; in others a flourishing colony developed. The plants grew on the track itself or in the vicinity of or on the large heaps of rubbish accumulated from the cleaning of cars. From time to time the rubbish was removed along with all the vegetation. In 1971, after 11 years of observation, no trace of *C. diffusa* was found. Until then one would have thought naturalization to be a fact. This is another classical case that shows how easily a railroad plant, persisting without difficulty on the same spot for more than a decade, can be wiped out. Eurasia.

Centaurea cyanus L.

Widespread, locally scattered, mostly in small colonies, rarely as unicates or in very large colonies. It is usually regarded as an escaped ornamental in the United States, but not as an introduced weed. This concept seems to fit the circumstances in St. Louis well. The colors of the flowers varied quite considerably from blue, which was the most prevalent, to whitish, pale pink, or purple. Often all these colors were represented in the same colony. These colors are, according to Hegi (1908–1931), frequently seen in the cultivated forms, but are rare or absent in wild forms. Naturalized. Eurasia.

Centaurea nigra L.

M 941, 16 June 1956; *M 1014*, 14 July 1956, 1 specimen each time; *M 1262*, 7 July 1957, a colony had formed by this time. The whole area was then cleared for a parking lot. G. Wagenitz has indicated that because of hybridization in the section to which these specimens belong determination was very difficult, and the plants are probably hybrids. The plants deviate from typical *C. nigra* especially in their phyllaries. The determinations are very uncertain. A similar situation has been found in Vienna by Rechinger (1950).

Centaurea stoebe L. subsp. **stoebe** (*C. rhenana* Bor.)

M 3613, Bremen Fr. Yd., 17 July 1971, 1 small colony. Determined by G. Wagenitz. Europe.

Centaurea maculosa Lam.

M 1816, 19 Aug. 1961 (US); *M 1852*, 10 Sep. 1961 (US), the same specimen. Although on both dates only branches were taken, no trace of this plant was seen the next year. Europe.

Centaurea diluta Ait.

MP, Lesperance St. Fr. Yd., *M* 3299, 14 June 1970; *M* 3348, 25 July 1970, 1 colony, ca. 12 specimens. Determined by G. Wagenitz. *Centaurea diluta* has previously only been reported from California in the United States. An inquiry in the seed firm next to the locality indicated that its warehouse received all its seed material from their headquarters in California in previous years, and this may pinpoint the source of this adventive. Mediterranean region.

Cichorium intybus L.

Widespread, locally frequent, in colonies of different sizes, sometimes huge, seldom as unicates. Once f. *albus* Neum. was recorded: *M 3403*, 2 Sep. 1970, amidst a colony of typical f. *intybus* with blue flowers. Naturalized. Eurasia.

Hypochaeris radicata L.

M 890, 30 May 1956, 1 specimen. Eurasia.

Picris hieracioides L.

*M*3377, MRS, Potomac St. and President St., 23 Aug. 1970, 4 specimens; *M 3650*, 1 Aug. 1971, 1 colony. Determined by R. P. Wunderlin. Eurasia.

Picris echioides L.

M 3300, Lesperance St. Fr. Yd. (MP), 14 June 1970, 5 specimens. Determined by D. M. Porter. Two specimens were left but no trace was found the next year, although the locality could be considered safe. Eurasia.

Tragopogon pratensis L.

M 1285, 21 July 1957, 1 colony. Europe.

Tragopogon dubius Scop. (*T. major* Jacq.)

Widespread, locally frequent in dispersed colonies of modest size, rarely as unicates. Flowering began in May and continued through July; afterwards some flowering heads could be seen on specimens which had already fruited. Occasionally in late autumn, through November, new flowering plants reappear. Naturalized. Eurasia.

Taraxacum officinale Weber

Widespread, locally frequent, for the most part in more or less dispersed colonies of different sizes. Flowering began in April and continued into November, but the amount fluctuated. *Taraxacum officinale* is much more frequent in the city then on the railroad. No doubt many dozens of the hundreds of the microspecies distinguished in Europe, especially by the Swedes, were represented, but no attempts were made to delve into this problem. It is odd, however, that *Taraxacum erythrospermum* Andrz. was never found, although many hundreds of *Taraxacum* plants were closely examined in the field. Naturalized. Eurasia.

Sonchus arvensis L. var. *glabrescens* Guenth.

Rare, observed in 5 regions in 13 localities, in small colonies and as unicates (2). In some places the plants persisted for some years, the longest time being 8 years; nevertheless they then disappeared without any obvious reason. Neither was there expansion of the sites. The passivity of S. *arvensis* on the railroad is remarkable, as in Europe it belongs to the most feared weeds (Hegi, 1908–1931). Fernald (1950) also mentions it in the U.S. as locally abundant. In 1971 the plant was seen only twice. Naturalized. Eurasia.

Sonchus oleraceus L.

Widespread, locally scattered. While the previous species was the rarest among the three introduced *Sonchus* species, S. *oleraceus* was the most frequent, mostly on open lots and margins, in small colonies or as unicates (8). Naturalized. Eurasia.

Sonchus asper (L.) Hill

Widespread, locally rare, observed 34 times. The colonies of it were especially small, often two or three specimens, and unicates were much more frequent (14) than in the other *Sonchus* species. Naturalized. Eurasia.

Lactuca serriola L. (*L. scariola* L.)

Widespread, locally frequent. It is a gregarious plant. No unicates were ever noticed, only colonies, which varied vastly in size. Naturalized. Eurasia.

Lactuca saligna L.

M 1071A, 8 Sep. 1956, 1 specimen. *M* 3382, 23 Aug. 1970, 1 specimen, also observed 14 June 1970 through Sep., 1 plant. No trace of it was found the next year. Eurasia.

Crepis pulchra L.

M 1453, 5 July 1958, 1 specimen. *M 1634*, 11 June 1960, 2 specimens; *M 1754*, 28 May 1961, 1 specimen, also observed in June. Although it seemed that *C. pulchra* had a good chance to persist, it disappeared without being exposed to any obvious danger of any kind, and it has not been observed since 1962. Eurasia.

Crepis tectorum L.

M 1807, 4 July 1961, 1 specimen (US). Eurasia.

DISCUSSION

Altogether 393 species were recorded (Table 3) in this study. Besides these, 53 infraspecific taxa were recorded. In 30 cases they were the only form of the species. In a few cases where a species was known to have a native and an introduced infraspecific taxon they were considered to be species for the statistical summary. In 23 cases 2 or even 3 introduced infraspecific taxa could be distinguished (1 subspecies, 13 varieties, 9 forms). Only one, mostly the prevalent or typical, was considered for the statistical accounts.

One question which arises is whether the synanthropic flora of the railroads in St. Louis is rich or poor? Although it might seem that this question could

easily be answered by a comparison with the findings of European adventive botanists, there is in fact very often no common basis for comparison. Previously published studies differ vastly in the length of time of the study, coverage of localities, inclusion of certain categories of plants, such as egasiophygophytes, archaeophytes, or doubtfully determined species. Furthermore, each additional year of observation may add new species.

Perhaps the best comparison can be made with the thorough 6-year investigation of the railroad station Zürich by Thellung (1905). Its geographical site, far away from oceans, is common with that of St. Louis. Altogether he recorded 451 introduced plants. One of the subgroups, the ergasiophygophytes is directly comparable in both places. In Zürich their percentage was 23.1%, in St. Louis 35.6% (138 species). This difference is at least partly explicable by inclusion in St. Louis of species of such genera as *Bromus*, *Festuca*, *Dactylis*, *Lolium*, *Phleum*, *Trifolium*, *Melilotus* into the ergasiophygophytes.

The richest adventive floras have been associated with seaports or inland harbors. The 800 species in 100 years in Montpellier (Thellung, 1912) has been the highest recorded number. In the United States Reed (1964) was able to discover 536 species during 10 years on chrome and manganese ore piles near Baltimore and Newport News, Virginia. In the famous Tweedside adventive flora (Hayward & Druce, 1919) 348 species were counted during 11 years. In Karlsruhe, Jauch (1938) was able to collect 247 species in 5 years (including some natives). Against this background the synanthropic railroad flora in St. Louis can be considered to be well developed, but more or less average.

The actual number of railroad synanthropes in St. Louis must be much higher than the reported 393 species. Thellung (1915) already cautioned that the investigation of an adventive flora is wholly based on chance. Lademann (1937) noted, after publishing a list of adventives in the Lusatia region in Germany, that the number of the adventives really occurring in the region was not nearly exhausted and that many a species had certainly evaded observation. These thoughts are frequently repeated in one or another way by many other botanists. There is no doubt that this statement is completely valid for St. Louis also. The best evidence is the high number of unicates (52) and single solitary colonies (75) found. This clearly means that many spots with unseen plants could simply have been missed.

In the following paragraphs some statistical data about the synanthropes are presented. First is the number in each of the eight regions.

The species were distributed in the regions as follows:

I: 274	II: 217	III: 195	IV: 152
V: 210	VI: 145	VII: 120	VIII: 149

The next comparison shows in how many regions the species occurred: 150 species occurred in only 1 region, 43 occurred in 2 regions, 26 occurred in 3 regions, 34 occurred in 4 regions, 19 occurred in 5 regions, 13 occurred in 6 regions, 28 occurred in 7 regions, and 80 occurred in 8 regions.

The majority of species were either widespread, occurring in all eight regions, or restricted and concentrated in only one region.

Frequency is demonstrated by the following: common 11, frequent 37, scattered 67, rare 70, very rare 208.

As mentioned before, the frequency categories were largely subjective, and because of the often great fluctuations in the number of synanthropes from year to year, it was often difficult to classify a particular species in a frequency category.

A group among the very rare plants merits special mention, namely, those which were seen only once. They were found either as unicates (47 species) or growing in a single colony of various sizes (52 species; 9 times, only 2 specimens were counted). Thus exactly one quarter of all the recorded synanthropes were seen only once. Further, 28 species (5 unicates and 23 colonies) were persistent, reappearing on the same spot repeatedly, 18 (7 unicates and 11 colonies) of them being woody species. Deducting the woody species, the survival of which is much more certain, unicates (45 species) persisted only twice (4%). On the other hand, plants growing in solitary (single) colonies (64 species) managed to survive in 15 cases (23%) for at least two years, and some for a decade and more. One should not forget that the unicates were victims of collecting. But in cases where only parts of a unicate were taken the results were no better. Therefore it is possible that the prospect for an introduced plant is much more favorable when its diaspores arrive simultaneously in quantities, thereby enabling it to create a colony immediately.

Many of the 393 synanthropes were novelties to the flora of Missouri. Until now 35 species and 4 infraspecific taxa had not been recorded previously. Altogether I added 129 new synanthropic taxa to the flora of Missouri (114 species, 1 subspecies, 11 varieties and 3 forms). The older data were reported in previous papers (Mühlenbach, 1957, 1960, 1969b) and in the *Flora of Missouri* by Steyermark (1963).

As have many adventive botanists, I analyzed the longevity of the synanthropes. As is usually done, biennials were combined with annuals. Calculation was not quite exact because in quite a few cases there are varying statements in the literature about the longevity of the plants in question. One plant is even described as "annual herb or perennial subshrub." For those plants the longer life span was used. Among 393 species, 254 were annuals, 107 perennials, 32 woody. These figures correspond fully with numerous European findings in the prevalence of annuals. The number of woody species in St. Louis seem somewhat higher than has usually been reported. The overwhelming majority of these woody species were ergasiophygophytes and, as this group was stressed in the field work, their representation may have been unusually high.

Statistics also reveal the botanical importance of single freight yards. The common plants were not especially suitable for this purpose, of course; therefore, only the very rare plants (208 species) were used for this analysis. Among the 30 freight yards, the highest yields were as follows: Carrie Ave. (RI) 37, Baden (MKT) 31, Lesperance St. (MP) 28, St. Louis Ave. (N&W) 25, North St. Louis (BN) 22, Lindenwood (SL-SF) 16. Of these same very rare plants, 116 species occurred in yards only, 50 occurred only along trunk lines, and 42 occurred in both places.

The 393 synanthropes belonged to 59 families, 28 of which were represented by only one species. The six families with the greatest number of species were Gramineae 74, Compositae 52, Cruciferae 28, Leguminosae 27, Caryophyllaceae 19, Polygonaceae 16.

The frequency of families in the various published adventive floras vary considerably, but the six families just enumerated, plus the Labiatae, are usually best represented. The Leguminosae frequently play a much more prominent role than in St. Louis, particularly when the introductions proceed chiefly from the Mediterranean region.

The most common genera in St. Louis were *Bromus*, *Eragrostis*, and *Polygonum* with 8 species each, and *Rumex*, *Chenopodium*, *Amaranthus*, *Silene*, and *Centaurea* with 7 species each.

Although authors differ quite often in the evaluation of the origin of many synanthropes, a summary shows that almost two-thirds of the St. Louis synanthropes are of European and/or Asian origin (Eurasian 180, European 44, Asian 39). Fifty-seven species are North American, 23 South American, 4 African, and 1 Australian. Three have a pantropic distribution and two, palaeotropic. The rest (40) are cultigens, many of them with uncertain provenances. Their number is much smaller than previously given. Omitted are some grasses, *Melilotus*, *Trifolium* sp., etc., when the introduction, rather than escape from cultivation, was most probable. The North American species originate for the most part in the western or southern part of the U.S. None are from the north—a situation often observed in European studies also. There is little doubt that the overwhelming majority of these synanthropes did not come here directly from their lands of origin, but stage by stage from intermediate stations. Only in the case of North American species was a direct introduction conceivable. Among the arrivals from other continents, only *Centaurea diluta* was possibly a direct introduction via California, as explained in the discussion of this species in the systematic part of this paper.

The overwhelming majority of the 393 recorded plants not native to Missouri flora are weeds. The definitions of the term "weed" have been numerous. Perhaps the most appropriate is that of Fogg (1945): "Any plant which grows where it is not wanted." Hardly another habitat will shelter so many weeds as railroad premises, although some ruderal places and dumps might come close.

It is of interest to compare the St. Louis railroad weeds with those of Missouri. Drew & Helm (1941) compiled a list of 154 representative Missouri weeds. They considered 135 species of primary and 19 of secondary importance. Of those 154 species, 79 were native and 75 adventive to Missouri. Of these 154 weeds, 146 were encountered at least once during this entire study of the railroads, only 8 were not seen. Three among these unseen species are introductions—*Lolium temulentum* L., *Stellaria graminea* L. and *Solanum dulcamara* L. Drew. Helm's list also contains *Solanum nigrum* L. (an introduced species), but there can be little doubt that the plant in question is actually the native *Solanum americanum* Mill. *Solanum nigrum* is neither mentioned in the *Flora of Missouri* nor has it been collected by me.

Some weeds are recognized as especially damaging to agriculture. The

Missouri seed law and regulations issued by the Missouri Department of Agriculture (1957, 1966) regulate the amount of so-called noxious weed seeds permitted in "agricultural seeds" of cultigens for sale. Altogether 15 weeds have been declared as noxious. With one exception (*Euphorbia esula* L.), they have been found on the railroads in St. Louis, many of them growing quite abundantly. Moreover four other species are classified as "prohibited weed seeds." These should never be present in any kind of agricultural seed that is for sale. Three of these are common on the railroads; only *Sorghum almum* Parodi has not been found.

The fate of the synanthropes on a railroad is usually dismal. For the most part they are doomed. An entire range of factors is implicated in this. Foremost is the reckless destruction by man.

The widespread use of weed killers is currently the strongest destructive influence. Track repairs, reconstruction, and relocation are also usually detrimental to railroad plants. The Luther Freight Yard (N&W) has been modernized to such an extent that except for some margins, practically nothing remains of the old yard. The O'Fallon Freight Yard with its interesting synanthropic flora was simply liquidated, sold, and converted into a parking lot. Similar examples could be multiplied. Accidents and frequent spills of oils and similar substances also often destroy railroad plants.

Of further great importance is the competition of the native plants and adverse climatic conditions. Climatic conditions in most cases decide whether an introduced plant will be able to reproduce. If synanthropes originate in warm regions, they may be unable to mature fruits in the shorter growing seasons. In other cases the ripened fruits cannot survive long, humid autumns and decay. In other cases prematurely germinating seed may be killed by frequent spring frosts. In numerous places the ground on the railroad is barren, and many plants may be unable to grow simply for this reason. However, it is also striking that many rarities which flower and ripen fruits before the close of the season and which grow in very remote, secure areas nevertheless vanish the following year. It seems that these circumstances work very selectively in the introduction process. With regular freight traffic many species are introduced again and again, but many never persist because they cannot adapt to the rigors of a railroad environment. For this reason, the number of introduced species should be much higher than it is in reality.

Plants which more easily adapt to altered climatic conditions and poor soils, which are stronger in competition with other plants, and which better tolerate damages become established on railroads and may be able to expand into the surroundings. Because of this, it is possible to observe introduced plants which may be able to hold out in the same locality for successive years or decades. Such plants have attained persistence. Many adventive botanists like to speak in such cases of naturalization, an often premature designation. For example, a spill of lubricant killed a vigorous colony of *Kickxia elatine* which had persisted for 16 years, and the wreckage of a derailed freight train buried a colony of *Arctium minus*. But, as already mentioned by Polunin (1960), colonies of long standing have also disappeared when absolutely no reason was obvious.

Much has been written about naturalization. Many have emphasized that it is possible to speak about naturalization only if the plant in question has shown an ability to transfer to some natural habitat, thereby proving that it is able to compete against the native plants, as well as having adapted to the climatic and edaphic conditions of its new homeland. It must be able to reproduce normally, without any assistance of man, be it by seed production or by vegetative means. Thellung (1915) also demanded that such plants be able to successfully outlive any climatic abnormality.

I confined my observations to the railroad premises, so that I have no personal observations of whether some synanthropes have gained a firm footing in natural habitats around the city and how they thrive there.

It is impossible to speak about natural habitats on the railroads themselves. During short periods of time small areas were relatively undisturbed, but these dwindled rapidly in number during the course of this study. For the most part the railroad premises border onto the built-up areas of the city. Extensive sections of the tracks run along the Mississippi River, but on the often narrow strip between the tracks and river bank no natural habitats remain. So the question of the naturalization had to be decided by observations on the railroads only, and it is on this basis that I have ventured statements on the eventual naturalization of synanthropes on the railroads in St. Louis. Two factors were decisive in my approach to naturalization. Scholz (1961) in his investigation of the ruderal flora in Berlin also spoke about naturalization, although very few natural habitats exist in a metropolis of this kind. He defined naturalized species to be those whose future extermination by man appears unlikely. For example, one species —*Sisymbrium irio* L.—persisted in Berlin on a very limited spot for 100 years, without expanding at all into its nearest surroundings. The neighborhood had suffered dreadfully during the war from the Allied bombing; however, the plant survived. Scholz noted that no great imagination would be needed to predict what would take place when the region, still partly in ruins at the time, was to rebuild. *Sisymbrium irio* would be completely finished. Such naturalization, as accepted by Scholz, is quite analogous with the situation on the railroad in St. Louis.

The second factor which encouraged me to speculate on this question is the existence of the modern *Flora of Missouri* by Steyermark (1963). While on the railroads all things may happen, in Missouri on the whole a common or frequent plant would be hardly exterminated, especially if it is widely dispersed. Steyermark rarely used the expression "naturalized" or its equivalent, "established." The most common definition about the distribution in Missouri was "throughout the state" or "throughout Missouri." The maps clearly depict the presence or absence in Missouri of every recorded plant in each of its 114 counties. Among the 89 species which I considered as naturalized, only 9 could be considered to be rarities, according to the *Flora of Missouri*. They are reported from five counties or fewer. However, all of them are doing fine on the railroads.

The judgment on naturalization was based on frequency, size of colonies, persistence in the same sites, number of years observed, location (margins are the safest places in the yards), and so on. Moreover, the estimate of frequency

and naturalization was independently repeated several times and the results compared. In most cases, naturalization could be taken for granted, but for some the determination was less certain. Altogether 89 species were classified as naturalized. The 89 naturalized species occurred in the eight regions as follows: 65 species occurred in 8 regions, 16 in 7 regions, 3 in 6 regions, 2 in 5 regions, 2 in 4 regions, and 1 in 2 regions.

The frequency of the naturalized species was as follows: common 11, frequent 32, scattered 42, rare 3, very rare 1.

The fact that the naturalized plants were widespread for 65 species and quite widespread for 16 species supports the idea that the respective species will survive permanently. In only a few cases were the naturalized plants more or less limited to a few regions, within which they were constantly abundant (especially *Apera spica-venti*, *Verbesina encelioides*). Only one species—*Dipsacus sylvestris*—was classified as a naturalized plant on the basis of a single, but huge, colony.

In a few cases naturalization may be mimicked when a plant that is unable to reproduce in its place of introduction is regularly brought in year after year. However, such a process of pseudonaturalization, although reported in the European literature [see Thellung (1918–1919) for the classical example of *Guizotia abyssinica* (L.f.) Cass.], seems to occur only with *Triticum aestivum* in St. Louis.

So-called trivialization has been observed in St. Louis. Thellung (1915) studied the changes which occur in the vegetation of artificial habitats after these habitats are no longer used. As a rule, synanthropes are overrun by native species and simply disappear, beginning with the annuals. This process was called trivialization by Thellung (1915). It was also observed and studied by Messenger (1968) on abandoned tracks and freight yards in England. In St. Louis both Ranken yards, originally used for holding yards for passenger trains, were abandoned. Many rarities, repeatedly found in these yards during their use, vanished after their abandonment.

It would, of course, be of interest to compare the St. Louis results with those for the other localities in the United States, but no published reports are known to me. However, H. H. Iltis (1965) kindly supplied a list of plants observed in Madison, Wisconsin, on the Illinois Central Railroad right-of-way, Mills and Spring Streets. The list contains 63 species, most of Old World origin. With three exceptions [two adventives, *Solanum dulcamara* L., *Hesperis matronalis* L. and one native, *Parthenocissus vitacea* (Knerr) Hitchc.] all were found in St. Louis also. This list confirms the opinion frequently expressed in Europe that there are plants which are especially fit for introduction and which appear in numerous places time and again. For example Kreh (1960) noted that species observed in Innsbruck (Austria) and Lucerne (Switzerland) also grow in Stuttgart. Furthermore, St. Louis (393) and Riga (128) have 45 synanthropes in common.

The yearly fluctuations in the number of species, as well as specimens, so frequently emphasized in Europe (Runge, 1965) was also observed in St. Louis. The following numbers illustrate this: From 1954 through 1960, 56 species had been seen that were never again seen. From 1965 through 1971, 61 species appeared that had previously never been seen. Several examples of "population

explosions" were observed. During the last years of this study *Chorispora tenella* and *Chaenorrhinum minus*, which had been rarities until then, developed huge colonies. It is premature to speculate about their fate, but the fact itself is noteworthy. One introduced grass, *Apera spica-venti*, as noted in the systematic section, behaved similarly, as did the native grasses, *Muhlenbergia asperifolia* (Nees & Meyen) Parodi and *Chloris verticillata* Nutt. (see below).

The opposite phenomenon—colonies persisting for years suddenly disappearing without apparent reason—was also observed and has also been frequently mentioned in European literature. One of the most striking examples was that of *Linaria vulgaris*, which grew in a very secure locality for eight years and then suddenly vanished. Also there is no doubt that during the years several scattered and rare species, e.g., *Agrostemma githago*, *Lepidium campestre*, *Solanum rostratum* and others, have become rarer than in the beginning. Sometimes the size of a colony may fluctuate considerably during the years. For example, *Centaurea diffusa*, which persisted for 11 years, produced from two specimens to quite large colonies from year to year.

Seed dormancy, which was already noticed by Brown (1880) in New York City's harbor, was observed in St. Louis also, especially in *Gaura sinuata*. Possibly seed dormancy is not at all a unique occurrence, but on railroads one normally must count on reintroductions, rather than seed dormancy. Very curious was the unexplained absence of *Potentilla argentea* for one year. It being a perennial, seed dormancy could not play any role.

The nanism of many synanthropes, which was especially stressed by Meyer (1931) and Brenan (1947), was also observed. Indeed, dwarfed forms of numerous species were common in St. Louis, and in this connection the name *Ammi majus* is a misnomer for specimens of this species collected on the St. Louis railroads.

As mentioned before, weed killing has had disastrous effects on railroad vegetation everywhere. The battle against vegetation on the railroads is almost as old as the railroads themselves. The reasons are manifold. It is carried out to improve the drainage of the tracks, to enable inspection of ties, fastenings, and switches, to prevent wheel slippage, to ease fire hazards, to facilitate the railroadmen's walking, to facilitate track maintenance and, to improve appearance. In addition there are laws concerning noxious weeds. The mechanical removal of plant cover prevailed in Europe until World War I. Quite popular in America was burning, which is now prohibited. The third possibility is to spray weed-killing chemicals. This began after World War I and gradually became more important. In the middle 1950s the application of weed-killing chemicals in St. Louis was already in use, although in some yards this practice was minimal, if even performed at all. When I began my work, the vegetation in the yards was usually largely unaffected. The increasing use of chemicals and its increasingly destructive effect on vegetation in St. Louis railroads has already been noted by me (Mühlenbach, 1957, 1969b). Since that time, the situation has become worse. Such places as the classification tracks of the large freight yards which initially yielded so many rarities are mostly bare of vegetation now. One interesting observation was made on *Eclipta alba*. In the 1960s it grew abundantly along

the classification tracks in the Carrie Ave. Freight Yard. After spraying it was undamaged while all other plants perished. It seems possible that lack of competition helped greatly in its spread. However, later it also disappeared, succumbing to some newer and more powerful weed killer. Survivors of spraying often show marked morphological changes making determinations often difficult. This was also observed by Kreh (1960), who considered the misshapen plants to be of interest to teratology.

Another trend, also observed in Riga, was quite marked. There are species which appear only as colonies. These may sometimes be quite dense, as with *Cardaria draba*. It is a perennial and the colonies might be easily created in course of time by subterranean rhizomes. However, such colonies also occur among annuals and biennials. Especially striking were the colonies of *Arabidopsis thaliana*. Not so compact are colonies of *Torilis arvensis*, *Pastinaca sativa*, *Lamium amplexicaule*, *L. purpureum*, *Plantago lanceolata*, *Anthemis cotula*, and *Lactuca serriola*. Gregariousness is very obvious, although these species may sometimes also appear as dispersed specimens. Some large and well-established colonies show very little tendency to expand. The large colonies of *Dipsacus sylvestris* and *Verbesina enceloides* were good examples. The tendency of several rare species to appear as single specimens has previously been noted. More than a dozen species could be enumerated, but a few examples will suffice. *Sisymbrium loeselii* was met 11 times, and 10 times it was a unicate. For *Lappula echinata* the numbers were 21 and 17, respectively; for *Eupatorium capillifolium*, 6 and 5. Finally some species are now and then found widely dispersed over a whole yard, mostly as single or a few specimens. Examples are *Silene noctiflora* and *Camelina microcarpa*.

Many European adventive botanists have emphasized that the clarification of the question of how the adventives arrived must be considered of utmost importance. What was the vehicle or agent which brought them in? They speak about citrus weeds, grain, bird seed, cotton, and wool adventives, and so forth. Besides a few obvious cases of plants introduced with vegetables and fruits through the St. Louis Produce Market and plants introduced with grain in the vicinity of grain elevators, no such exact sources could be pinpointed in this study.

In Europe certain plants have been identified as migrant plants (Scheuermann, 1930), plants that may not only be brought in on freight but that can also spread by natural means along suitable railroad sites. These were called ferroviatic migrants by Domin (1947). Very clear examples have been given in Denmark by Pedersen (1955). Perhaps the best known species in this connection is *Eragrostris minor* (Galenieks, 1953–1959). However, clear examples have not been discovered in St. Louis.

The question of immigrant plants—those which are actively dispersing themselves independently of railroads—has not been settled in my study. Such immigrant plants must from time to time cross railroads and gain a foothold there. Among the aliens in St. Louis, some are probably immigrants. However, it is not easy to identify these with certainty without thorough data throughout a very large geographical area, not only the railroads. Certainly nothing like the explo-

sive spread in Europe of *Senecio vernalis* Waldst. & Kit. (Ascherson, 1862) or the sudden dispersal of S. *tubicaulis* Mansf. to the polders of the Ijsel Meer in Holland (Schroeder, 1969) has been documented. Plants such as *Setaria faberi* and *Viola kitaibeliana* which are said by Steyermark (1963) to be actively spreading in Missouri might be considered migrant plants, but detailed information is lacking.

Scheuermann and many others simply ignored classification tracks in railroad yards, concentrating their attention primarily on unloading sites, warehouses, etc. They did not expect to find truly introduced adventives on classification tracks. My experiences led me to opposite conclusions. It is unthinkable that all the plants I found along classification tracks were only migrants. Where would they have migrated from and what long distances would they have to traverse in order to produce the frequently observed unicates? The whole procedure on classification tracks (as described previously) seems to be well adapted for the ready dispersal of the hitchhiking diaspores, and, consequently, the importance of the classification tracks for adventive botany remains high. They have had a major part in the dispersal of synanthropes in the past. At the same time, the current emphasis on chemical weed killing ensures that arriving diaspores have little chance of survival. Although the switching work is the same as it was 20 years ago, the results from the botanical point of view are now, as a result, nearly nil.

The unusual and sudden appearance of certain plants in several widely separate localities in certain years which were afterward never seen again is an interesting but unexplained phenomenon. This happened with the introduced *Galeopsis tetrahit* in 1956, *Ranunculus sardous* in 1970, and with the native *Senecio glabellus* in 1961. The most remarkable occurrence of this phenomenon was observed for the native *Senecio glabellus* Poir. The genus *Senecio* is very rare in St. Louis and so each observation immediately attracted attention. This species was discovered on May 20 through 28, 1961, in six localities in three regions. In all localities only a single dwarf specimen was found. Not a single specimen was ever found again.

Another notable phenomenon was frequent joint occurrence of species pairs such as *Sida spinosa* and *Abutilon theophrasti*, *Trifolium pratense* and *T. repens*, and *Salsola collina* and S. *kali*.

This work pinpointed some taxonomic problems. In the case of *Artemisia vulgaris* and *Chenopodium glaucum* three and two varieties, respectively, were identified from a few plants collected in nearly the same location. In cases such as this it seems very unlikely that distinct infraspecific taxa could appear simultaneously as synanthropes. An incorrect evaluation of taxonomic status seems more likely.

Altogether 476 native species were collected during this study. Many were common but quite a few were rarities. Undoubtedly many more existed, as some frequently encountered plants such as *Platanus occidentalis* L. were not collected, and undetermined collections were also not counted. A certain number must also have been overlooked. One noteworthy observation is that many native plants were observed only as single colonies (65) or even as unicates (25). Only

a few of the 65 colonies survived in the same spot through the years. It is my firm conviction that many of these native plants in freight yards were introductions like the true synanthropes. Many were conspicuous [e.g., *Boerhaavia erecta* L., *Asclepias tuberosa* L., *Liathris pycnostachya* Michx., *Astranthium integrifolium* (Michx.) Nutt.]. They were all found in much frequented areas, and in the terminology of Thellung must be considered to be apophytes. Seed dormancy could be assumed in at least one case. *Schrankia nuttallii* (DC.) Standley suddenly appeared along old cleanout tracks abandoned for several years in the Baden Freight Yard. Or did it, as well as many other species, appear here by introduction or by ferroviatic migration? This question cannot be answered directly. That natives of Missouri can be introduced in St. Louis by traffic is clearly seen in Steyermark's *Flora of Missouri*. He cited a long series of species with widely separated localities from different parts of the state. No intermediate stations were known. This indicates that we are dealing with introductions, not with ferroviatic migration. The following 14 species were plants native to some parts of Missouri, but considered by Steyermark (1963) to be introductions in St. Louis. Almost all originate in the western and/or southern parts of the state, quite a few being more or less restricted to the loess mounds of the most northwestern counties. They all are apophytes in the sense of Thellung.

1. *Sporobolus cryptandrus* (Torr.) Gray. Quite widespread, locally scattered.

2. *Chloris verticillata* Nutt. Three colonies were observed in Regions 1 and 8. Two of them persisted for some years—1959–1966 in the North St. Louis Yard, 1966–1971 in the Baden Yard. Quite unexpectedly a rapid spread occurred in South St. Louis, especially in the vicinity of the Christy Park from 1966 to 1972, and this grass has now spread rather widely in the city. It is likely to become a pest in the future. The entire mature inflorescence breaks off and is blown around like a tumbleweed. The grass was first encountered as a tumbleweed in Region 4, but a careful search of the surroundings revealed nothing. It is clear that the tumbleweeds of this species may travel quickly and far. It is worthwhile to mention that the dead end of the tracks of the MP Christy Lead, serving the Christy Works Refractories Division of the H. K. Parker Company and its underground clay mines, approached Christy Park within 100 m. The works were demolished and the tracks were dismantled in 1969; but it is of course impossible to say whether the phenomenal spread of *Chloris verticillata* was brought about by a railroad introduction.

3. *Andropogon saccharoides* Swartz. At least 8 colonies were observed in Regions 1 and 5, most of them persistent. One was observed from 1954 to 1971.

4. *Scirpus divaricatus* Ell. Only one collection was made: *M 980*, 1 July 1956.

5. *Portulaca mundula* Johnston. *M 1116*, 7 Oct. 1956, and again seen 4 Aug. 1963.

6. *Cleome serrulata* Pursh. Unicate, but collected piecemeal three times *M 1790*, 1 July 1961; *M 1838*, *M1806*, 29 July 1961; *M 1838*, 9 Sep. 1961.

7. *Ribes odoratum* Wendland f. *M 1365*, 1 shrub, 14 Sep. 1957.

8. *Liquidambar styraciflua* L. Four localities in Regions 1 and 6. Mostly in shrubbery accompanying the tracks. Ripe fruits and quite low juvenile shrubs were seen.

9. *Trifolium carolinianum* Michx. *M 195*, 27 June 1954, unicate.

10. *Euphorbia marginata* Pursh. Scattered in 6 regions, in quite a few places persistent. Steyermark (1963) considered it as escaped from plantings in gardens. Along the railroads in St. Louis many localities were far away from gardens.

11. *Passiflora incarnata* L. Three locations in Regions 2 and 8, forming small colonies. It persisted in one locality from 1966 to 1971, although it could not be found in 1967.

12. *Gaura coccinea* Pursh. *M 632*, 18 June 1955, unicate. *M 1605*, 15 May 1960, 1 colony; *M 1640*, 18 June 1960; *M 1737*, 21 May 1961.

13. *Cynosciadium pinnatum* DC. *M* 938, 16 June 1956, 4 specimens.

14. *Iva xanthifolia* Willd. Observed seldom in 4 regions (1–3, 5) with a pronounced tendency to appear as unicates (10). The height was ordinarily low.

There is no doubt that the great majority of the synanthropes is introduced by the cargo of freight trains, but in rare cases the freight cars themselves are vehicles for hitchhiking diaspores (Zimmermann, 1907; Pedersen, 1955; Hugentobler, 1961). In 1974 I confirmed this after examining various freight cars. Seeds were collected from the sticky layer of lubricants which usually covers the lubricating cups of wheels. In three hours perhaps 30 seeds were collected. Most seeds were anemophilous, most probably of the composite family. Frequently only the pappus was collected, the achenes beng already detached. Grass spikelets were also collected, although some were disintegrated. Freight cars have several cavities or pockets, where something unusual may also be found. Some totally dried ligneous branches, a piece of a corn cob, some grain seeds, and other fragments of plants were removed. Seeds were also found in the runners of sliding doors. These seeds were found primarily on box cars but also on hoppers and flat cars. Of course, these seeds could not be considered sure introductions. They could as well have been picked up in St. Louis; however, the potential clearly exists. Such seeds can drop off the cars due to vibration (Pedersen, 1955) or during cleaning or lubrication. Whether contact with lubricants would suppress germination is not known.

It was obvious that almost all seeds were found on the car trucks of the older type. Just as with the development of the weed killers, introduction of the so-called roller bearings on new railroad cars has also diminished the chance of dispersal of plants by the railroads.

Railroad workers themselves may also play a major role in the dispersal of plants on the railroads. This may be demonstrated in two ways. From time to time plants never seen before (*Chaerophyllum tainturieri* Hook., *Verbena urticifolia* L., *Specularia perfoliata* (L.) A. DC., *Solidago* sp., *Erigeron strigosus* Muhl., *Rudbeckia hirta* L.) suddenly appeared in my backyard. Most of these plants are frequently encountered on the railroads. I often found different seeds and fruits in abundance in the cuffs of my trousers or attached to my socks after excursions. Perhaps the most frequent were the spikelets of *Bromus tectorum*, brought home now and then in large amounts in the early summer. More annoying were *Setaria verticillata*, *Galium aparine* and different *Desmodium* and *Bidens* species. Quite seldom fruits of *Cenchrus longispinus* (Hack.) Fern., *Tribulus terrestris* L. and *Xanthium strumarium* L. may be attached to clothing.

It is likely that all were effectively dispersed from the railroad on my clothing. Therefore it seemed logical as the next step to investigate the cuffs of a switching crew, who spent long times outdoors in a railroad yard. In the North St. Louis Freight Yard many seeds and fruits were indeed found after such an examination in 1974. The probability seems great that the railroadmen participate effectively in the dispersal of plants in freight yards. This has been called epianthropochory (Faliński, 1972). It is especially credible when rare plants are spread over a whole yard as many isolated specimens.

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ANNALS
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VOLUME 66 1979 NUMBER 2

FLORA OF PANAMA[1]

BY ROBERT E. WOODSON, JR. AND ROBERT W. SCHERY
AND COLLABORATORS

Part IV

FAMILY 58A. BASELLACEAE

W. G. D'ARCY[2]

Perennial *herbs* or *vines*, stems slender or stout and fleshy, glabrous; rhizomes sometimes bearing fleshy tubers. *Leaves* alternate, entire, often fleshy, sessile or petiolate, exstipulate. *Inflorescences* spikes, panicles or clusters, the flowers sessile or short pedicellate, bracteate, bracteoles 2 or 4, forming a calyxlike receptacle, sometimes accrescent. *Flowers* regular, hermaphrodite or perhaps sometimes unisexual, the perianth of 5 sepals somewhat united basally, imbricate; stamens 5, inserted on the petals, sometimes basally connate, the anthers introrse, 4-locular; ovary superior or ½ inferior, 1-locular, the ovule solitary, basal, erect, campylotropous, the styles 3, terminal, united or not, the stigmas 3 or 1. *Fruit* dry or baccate, sometimes winged by the expanded perianth; seeds with bent or spiral embryo, perisperm sparse.

The Basellaceae includes five tropical genera, four of the New World, and only *Basella* in the Old World. The family has been allied with the Caryophyllaceae and Chenopodiaceae. Its closest affinities may be with the Phytolaccaceae.

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[2] Missouri Botanical Garden, 2345 Tower Grove Avenue, St. Louis, Missouri 63110.

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a. Flowers distinctly pedicellate, strongly scented; perianth mostly opening wide to display the anthers; fruit samaroid, flat, white, dry; rhizomes tuber bearing ..... 1. *Anredera*
aa. Flowers mostly sessile, scarcely scented; perianth united to above the middle and partly closed around the anthers; fruit baccate, subglobose, nearly black, juicy; rhizomes without tubers ..... 2. *Basella*

1. ANREDERA

Anredera Juss., Gen. Pl. 84. 1789. TYPE: *A. spicata* J. F. Gmelin = *A. vesicaria* (Lam.) Gaertn. f.

Boussingaultia H.B.K., Nov. Gen. Sp. Pl. 7: 194, *tab. 465 bis.* 1825. TYPE: *B. baselloides* H.B.K. = *Anredera baselloides* (H.B.K.) Baill.
Siebera Presl. in Oken, Isis 21: 275. 1828. TYPE: *S. baselloides* Presl. Not seen, fide Index Kewensis.
Clarisia Abat, Act. Soc. Med. Seville 10: 418. 1792; ex Spreng., Gen. 1: 202. 1820. in syn. nomen Rejic. vs. *Clarisia* Ruiz & Pavon (1789)—Moraceae.
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Tandonia Moq. in DC., Prodr. 13(2): 226. 1849. TYPE: not designated.
Clairisia Benth. & Hook. f., Gen. Pl. 3: 78. 1880. in syn. *Clarisia* Abat. orth. mut.

Vines climbing on shrubs, glabrate, mostly slender; rhizomes sometimes with fleshy tubers. *Leaves* ovate or elliptical, sometimes succulent, sometimes drying dark, pinnately few veined; petiolate; exstipulate. *Inflorescences* axillary, sometimes more or less terminal sparingly branched, lax racemes, the pedicels short, slender, subtended by linear bracts, the flowers subtended by 2 or 4 decussate sometimes basally connate bracteoles. *Flowers* perhaps sometimes unisexual, perianth 5-parted, basally connate; stamens 5, inserted at the base of the calyx lobes, the anthers oblong, versatile, basifixed; ovary globose or ovoid, 1-locular, sometimes partially partitioned, with 1 basal, campylotropous ovule, the styles basally united, short, the stigmas 3, linear or clavate, sometimes only small porrect lobes on the style, sometimes bifid. *Fruit* globose, enclosed by the perianth, sometimes samaroid within the accrescent bracteoles; seed reportedly globose or reniform.

Anredera in the strict sense is monotypic with only the species treated here. However, recent writers follow Baillon (1888) and van Steenis (1957) in uniting with *Boussingaultia* H.B.K. and *Tandonia* Moq., which have subglobose rather than samaroid fruits. Van Steenis stressed that the accrescence of the perianth in fruit is the only feature which separates these elements, and that shape of style branches and other features relied upon by Moquin and Hauman (1923–5) sometimes are not even of specific import. Van Steenis' designation of *Anredera baselloides* (H.B.K.) Baill. as lectotype of sect. *Tandonia* (Moq.) Volk. (not in Panama) cannot be accepted as Moquin placed this species in a different genus. *Boussingaultia*. An acceptable lectotype is still to be designated.

FIGURE 1. *Anredera vesicaria* (Lam.) Gaertn. f.—Habit (×⅝).—B. Leaf (×⅝).—C. Flower (×7½).—D. Flower with bracts moved to the side and front petal turned down (×7½).—E. Ovary (×15). [After *Seemann 310* (K).]

1. **Anredera vesicaria** (Lam.) Gaertn. f., Fruct. Sem. Pl. 3(2): 176, *tab.* 213. 1807.—Fig. 1.

Anredera scandens sensu auct., not *Polygonum scandens* L. 1753.
Basella vesicaria Lam., (1785) Encycl. Méth. Bot. 1: 382. 1785. TYPE: Cultivated Paris, stock from Peru, *Lamack*, not seen.
Anredera spicata Gmelin, J.F. Syst. Nat. 2: 454. 1791. TYPE: not seen.
A. cumingii Hassk., Flora 48: 401. 1865. TYPE: not seen.
Gomphrena volubilis Blanco, Fl. Filip. 199, ed. 2: 140. 1845; ed. 3. 1: 252. 1877. TYPE: not seen.

Vines, festooning fences and shrubs, glabrous, stems mostly slender, green or purplish; roots tuberous. *Leaves* alternate, elliptical, slightly succulent, apically acuminate, basally obtuse to cordate, to 6 cm long, the costa with ca. 3 veins alternating on each side, the minor venation obscure; petioles 4–15 mm long. *Inflorescences* axillary to terminal, erect or somewhat pendant, 3–15 cm long, mostly lax unbranched racemes, the rachis slender, naked for the first 10 mm, open or appearing somewhat congested in fruit, evenly cylindrical, the flowers mostly blooming at once; pedicels slender, ca. 1 mm long, subtended by a linear bract, the flowers subtended by 2 minute, cucullate, acute often basally connate bracteoles, and by 2 inner, basally accrescent bracteoles which reach more than halfway up the flower bud. *Flowers* strongly scented, perhaps sometimes unisexual, white, calyx 5-parted, the sepals thin, ovate, basally connate; stamens 5, inserted at the base of the calyx lobes, the filaments slender, the anthers oblong, narrow, and curved, basally bifid, dorsifixed; ovary subglobose or ovoid, the stigma short, the styles 3, slightly clavate, entire, emarginate or 2-cleft, papillose. *Fruit* samaroid, discoid, the 2 inner bracteoles accrescent and enclosing the perianth and sexual parts, forming broad, reticulate, stramineous wings; seed not seen.

Anredera vesicaria may be recognized by its white, fragrant cylindrical racemes of flowers and winged fruits. The tubers are reportedly of medicinal value in Peru. Probably a native of South America, the species is sparingly but widely cultivated and is naturalized in many tropical areas. It has been collected only once in Panama in spite of intensive efforts in recent years to relocate it. It is known from the Antilles and from other Central American countries.

PANAMA: Near Panama City, *Seemann* (K).

2. BASELLA

Basella L., Sp. Pl. 272. 1753; Gen. Pl., ed. 5. 133. 1754. TYPE: *B. rubra* L. = *B. alba* L.

Gandola L., Sp. Pl. ed. 2. 380. 1762. in syn. Based on *Gandola alba* and *G. rubra*, Rumphius, Herb. Amboinese 5: 417. 1747. TYPE: Indonesia, not seen.

Herbs or *vines*, stems sometimes thick and succulent, glabrous; roots not tuber

→

Figure 2. *Basella alba* L.—A. Plant 2 months old: arrow indicates where stout stem narrows abruptly into a slender vine (×½).—B. Cleistogamous flower (×2).—C. Open flower (×2). [After *D'Arcy 10506* (MO), cultivated, Missouri Botanical Garden.]

B
C
A
J.E.K.
J.E. Klein

bearing. *Leaves* alternate, sessile or short, fleshy, entire. *Inflorescences* terminal or axillary spikes, lax or erect, crowded or open, the rachis thick or thin, the flowers sessile or pedicellate; bracteate; bracteoles 2, enclosing the base of the flower. *Flowers* with 5 sepals basally united, imbricate, urceolate, somewhat fleshy, pink, red, or white; stamens 5, the filaments short, straight in bud, inserted on the sepals, basally broadened, the anthers dorsifixed, extrorse, dehiscing longitudinally; ovary sessile, 1-locular but sometimes partly partitioned, the styles slender, 3. *Fruit* purple black, baccate, the perianth parts colored, succulent, and enclosing the ovary and the seed; seed subglobose, the embryo spiral or folded.

Basella is an Old World genus of 5 species, one of which is widely cultivated in the tropics for food and has escaped and naturalized in parts of the New World. Three species are endemic to Madagascar and one, *B. paniculata* Volkens, is localized in southeast Africa.

1. **Basella alba** L., Sp. Pl. 272. 1753. TYPE: not seen.[3]—FIG. 2.

B. rubra L., Sp. Pl. 272. 1753. TYPE: not seen.
B. nigra Loureino, Fl. Cochinch. 183. 1790. TYPE: not seen.

Succulent glabrous *herb* becoming a slender, twining *vine*, the stems at first stout, to 2 cm thick, green, after several months of growth and attaining height of 15–45 cm, narrowing, sometimes abruptly and becoming slender, elongate and climbing. *Leaves* sessile or short petiolate, 4–7 cm long, entire, fleshy, ovate, often broadly so, the juvenile leaves often larger, apically rounded, obtuse or acute, basally cuneate, truncate, or cordate, the lateral venation somewhat obscure, ca. 5 veins on each side, minor venation obscure; petioles stout, to 8 cm long or wanting. *Inflorescences* axillary or subterminal spikes to 15 cm long, the rachis stout or slender depending on the maturity of the plant; flowers subsessile or pedicellate on juvenile forms, situated on the apical portion of the rachis; bract scalelike; bracteoles calyxlike, 1–2 mm long, acute. *Flowers* perfect, sepals white, pink, or red, 3–5 mm long, united to above the middle, urceolate to cylindrical, the 5 lobes broad, short, cucullate; stamens included, inserted at the base of the perianth lobes, the filaments short, the anthers cordate, included; ovary conical, 1-locular, sometimes partitioned, the 3 styles slender, papillose pilose. *Fruit* a dark purple or black baccate drupe, the perianth parts enlarged, succulent and enveloping the globose seed and ovary.

Basella alba is cultivated in various parts of the tropics as Ceylon or Malabar spinach or espinaca de China o de Malabar. It is cooked as a pot herb, the flavor like that of spinach (*Spinacia oleracea*) but with a slimy texture. In some countries the berries are used to color foodstuffs. In Panama it is cultivated in Chinese market gardens in the Canal Zone and by inhabitants of eastern Panama where it escapes and is perhaps naturalized. The change in growth form from

[3] For a list of synonyms see Steenis (1957). Only these names have been used for Panamanian plants. Steenis indicates Graham, Cat. Bombay 170. 1839 was the first to unite *B. rubra* under *B. alba*, but he suspected that such action might have been taken earlier, perhaps using the name *B. rubra*.

a stout-stemmed erect herb to a slender climbing vine after a few months growth is abrupt and dramatic. There are changes in the shape of the inflorescence and flowers as well.

CANAL ZONE: Cultivated, Chinese garden along Thatcher Highway 1 m W of Rodman Naval Station, *Nee 10424* (MO, PMA). DARIÉN: Río Chico upriver ca. 1 hour by outboard from Río Chucunaque, *Burch et al. 1125* (MO). Weed near Yaviza, *Gentry & Mori 13496* (MO, PMA).

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Numbers in **bold face** type refer to descriptions; numbers in roman type refer to synonyms; numbers with daggers (†) refer to names incidentally mentioned.

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FLORA OF PANAMA[1]

BY ROBERT E. WOODSON, JR. AND ROBERT W. SCHERY
AND COLLABORATORS

Part IV

FAMILY 73A. CAPPARACEAE-TOVARIOIDEAE

W. G. D'ARCY[2]

Erect or sprawling *herbs*, *shrubs*, or small *trees* (Lagerheim), fetid, glabrate; sap clear; stems branching. *Leaves* alternate, trifoliolate, the leaflets narrow, pinnately veined, subsessile; petiole long and slender; exstipulate. *Inflorescences* lax terminal racemes, the pedicels slender, subtended by somewhat distant narrow bracts. *Flowers* perfect, green, white, or yellow (6–)8(–9)-merous, the calyx lobes free, lanceolate to elliptic, glabrous, pulverulent or ciliate, petals oblong, stipitate; stamens inserted on a rudimentary disc, alternating with minute nectaries, the filament pubescent, sometimes expanded and differentiated basally, sometimes unequal, the anthers ovate, basifixed, somewhat hastate, the apex (not the connective) sometimes differentiated into a point, papillose or sometimes minutely pubescent, longitudinally dehiscent; pollen tricolporate; ovary ellipsoidal to globose, imperfectly 6–8 locular, the placenta axile, protruding as arms into the locule, the ovules campylotropous, numerous; style stout or obsolete, the stigmas 6–8, short, dark hornlike processes. *Fruit* a subglobose berry, the style and the stigmas usually persistent, the calyx usually deciduous; seeds small, numerous, reniform, the embryo curved, surrounded by scant endosperm.

The Tovariaceae comprises one genus, *Tovaria*, widespread in tropical America, in the Antilles known only from Jamaica. Plants of this group were first published in the Capparaceae, and were recognized as a tribe, Tovarieae, of that family by Triana and Planchon (1862). Eichler (1889) assigned the genus to the Papaveraceae, and Pax (1891) placed it in a family of its own where most textbooks now treat it, although Metcalfe and Chalke (1950) accepted *Tovaria* as a member of the Capparaceae without noting any reservations. It supposedly differs from other Capparaceae in its pleiomorphic central placenta, in its globose fruit, and in anatomical details alluded to but not contrasted by Lagerheim (1892). In aspect and form of the leaves and inflorescence it is similar to other genera of the Capparaceae, e.g., *Cleome*, *Polanisia*, etc., tending to become woodier than these but not more so than other members of the family. The central placenta is approached in the axile placenta of *Styxis* (= *Roydsia* Roxb.) (see Lotsy 1911) which has 3 locules in contrast to the usual 2 locules in Capparaceae and 6–8 locules in *Tovaria*. Lagerheim's study showed the seeds and embryogenesis to be fundamentally similar in the Capparaceae and Papav-

[1] Assisted by National Science Foundation Grant DEB 77-04300 (W. G. D'Arcy, principal investigator).

[2] Missouri Botanical Garden, 2345 Tower Grove Avenue, St. Louis, Missouri 63110.

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eraceae with a trend to reduction of nucellus becoming more pronounced in the Cruciferae and Resedaceae, two other related families. In this respect he found *Tovaria* to be somewhat intermediate between the Capparaceae and Papaveraceae. Meager pollen information (Erdtmann 1952) to date and chemical data (Hegnauer 1973, Gibbs 1974) support affinity with or placement within the Capparaceae and argue against proximity to the Papaveraceae. *Tovaria* finds many plants of similar general appearance in the Capparaceae and strong odors are also common in that family. No members of the Papaveraceae have even vaguely similar form. The Papaveraceae are also distinguished from the Capparaceae including *Tovaria* by colored sap, bluish overall cast, lack of myrosin cells, and other features which Cronquist (1968) believed reflect a considerable phylogenetic distance between the two families. Mauritzon (1935) suggested that secretory cells in the parenchyma of *Tovaria* might be homologous with the latex tubes of the Papaveraceae, but this suggestion has not met subsequent endorsement. Goldblatt (1978) found the chromosomes of *Tovaria* to be n = 14, a number reported in two genera of Capparaceae. On balance, there is good evidence for including *Tovaria* in the Capparaceae and little for placing it near the Papaveraceae. Its affinities are best indicated by recognizing it as a subfamily, Tovarioideae, of the Capparaceae.

Literature:

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Triana, J. J. & J. E. Planchon. 1862. Prodr. Fl. Novo-Granat. Ann. Sci. Nat. sér. 4. 17: 88.

TOVARIA

Tovaria Ruiz & Pavón, Prodr. 49. 1794. nomen cons. not *Tovaria* Adanson (1763), Polygonaceae, not *Tovaria* Necker (1790), Liliaceae, illegitimate,

see International Code of Botanical Nomenclature, 1978, Art. 20. TYPE: *T. pendula* R. & P.

Bancroftia Macf., Fl. Jamaica 1: 112. 1837. TYPE: *B. diffusa* Macf. = *Tovaria diffusa* (Macf.) Fawc. & Rendl. non *Bancroftia* Billb. 1833. (Umbelliferae).

Only two names have been published in this genus, *T. pendula*, the type, and *T. diffusa*, which was described from Jamaica. Fawcett & Rendle (1914) distinguished *T. diffusa* from the mainland plants on the basis of narrower, relatively longer sepals, and a sessile stigma. Examination of several collections from Jamaica did not confirm Fawcett & Rendle's sepal distinction, as both sepal shape and length are quite variable with the age of the flower, and the Jamaican plants appeared quite within the range of mainland morphology. Only one collection, *Proctor 34258* (IJ), was available with mature fruits, and its style is extremely short, more or less supporting the Fawcett & Rendle observation on a sessile stigma. Such short styles were not observed on any mature fruits from mainland America. However, on several Jamaican collections ovaries which had not expanded to full fruiting size bore styles similar in length to those of mainland plants. The difference in style length, therefore, appears to be a matter of elongation in fruit rather than any evident difference in the flower. If this difference in fruiting style is pervasive amongst the Jamaican populations, then these plants probably warrant taxonomic distinction, but perhaps not at the species level. In any case, the name *T. diffusa* does not apply to collections seen from mainland America, many of which had been determined with this name rather than the earlier *T. pendula.* It may be possible to separate mainland populations into more than one taxon, but this study uncovered no basis for doing so.

1. **Tovaria pendula** Ruiz & Pavón, Syst. Veg. Fl. Peruv. Chil. 85. 1798; Fl. Peruv. Chil. 3: 73, *tab. 304.* 1802. TYPE: Peru, *Pavón* (MO).—FIG. 1.

Erect or sprawling vinelike *herbs* or *shrubs* to 1.5 m tall (Panama), rarely *trees*, glabrate, fetid, sap clear; stems branching, terete but with numerous fine lines. *Leaves* alternate, trifoliolate, the leaflets ovate to lanceolate, to 15 cm long, 3.5 cm wide, the middle leaflet largest, apically acute or acuminate, basally obtuse, the lateral leaflets somewhat oblique, entire or minutely crenate, the costa stramineous, the lateral nerves 20–30 on each side, sometimes not distinct from the reticulate minor venation, arcuate, anastomosing near the margin, subsessile; petioles slender, erect, mostly 3–5 cm long, sometimes minutely puberulent near the base. *Inflorescence* an elongate, lax open terminal raceme to 20 cm long, the pedicels slender, ca. 15 mm long, subtended by linear bracts 2–8 mm long which arise slightly below the point of pedicel insertion; rachis mostly subterete, glabrous or minutely puberulent. *Flowers* greenish, white, or yellow, 6–8-merous, the calyx lobes lanceolate to ovate, 3–5 mm long, sometimes minutely ciliate; petals oblong or elliptical, stipitate, basally ciliate and sometimes basally pubescent ventrally; stamens inserted on a small dark disc which is produced into minute nectaries between the stamens, the filaments flat, broadened in the lower ½, pilose on the edges and dorsal side of the broadened portion, basally glabrous

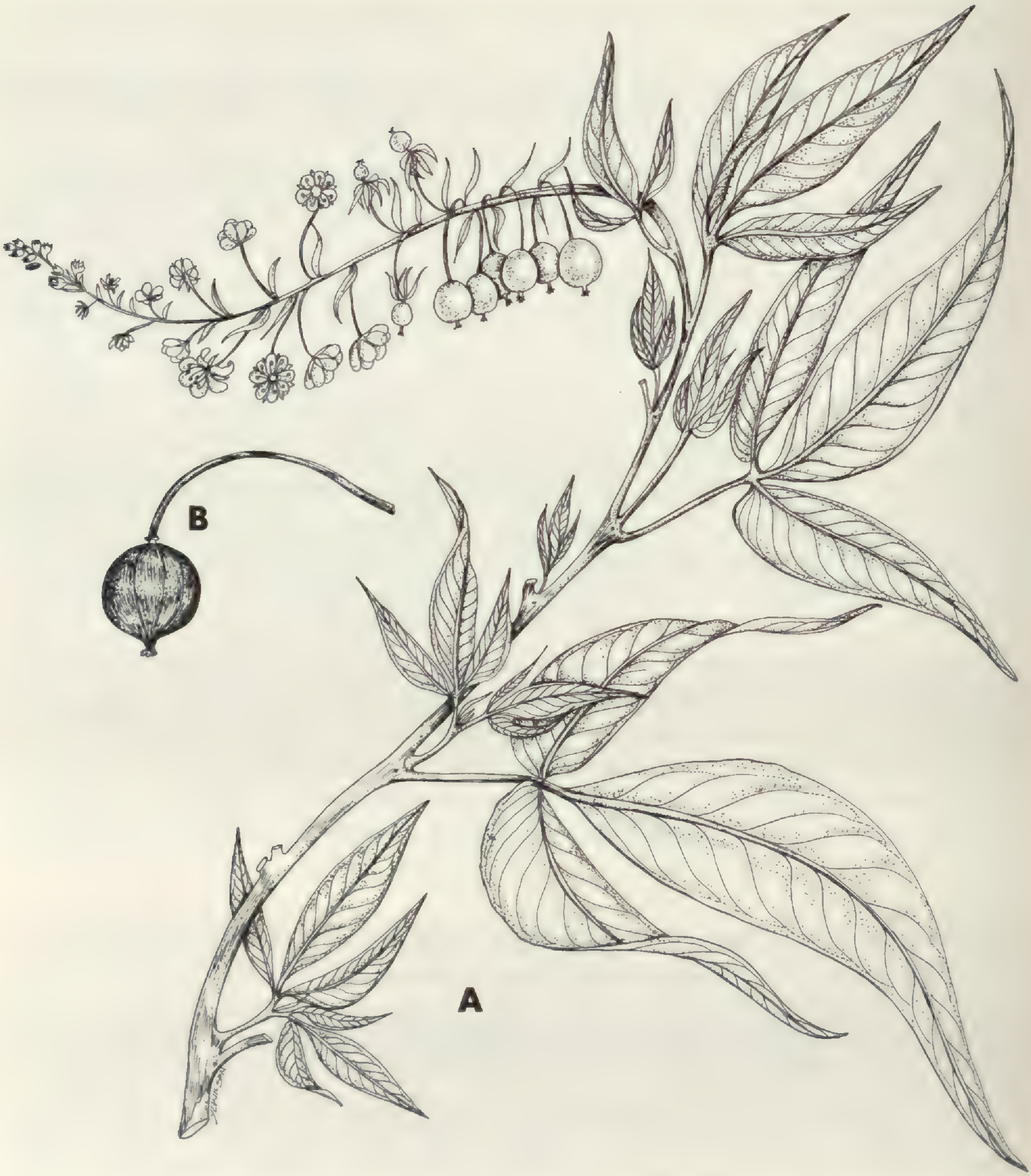

FIGURE 1. *Tovaria pendula* Ruiz & Pavón.—A. Habit (×½). [After *Croat & Porter 16061* (MO)].—B. Fruit (×1). [After *Mori & Kallunki 6023* (MO)].

and sometimes differentiated, 1–1.5 mm long at the anthesis, the anthers ovoid hastate, 1–2 mm long, basifixed and subversatile, dehiscing longitudinally and partially curling, papillose or minutely pubescent, especially dorsally, apically drawn into a minute beak; ovary ovoid, 1-locular but partially separated into 6–8 chambers by the axile placentas, the ovules numerous, the style stout, the stigmas 6–8 short, dark, hornlike processes. *Fruit* a slimy berry ca. 1 cm across, subglobose, topped by the persistent, peglike style and the patent stigmas, stipitate on the disc; seeds minute, compressed, reniform, smooth, reddish brown, 0.8 mm across, immersed in the white-drying pulp.

This species is recognizable by its trifoliolate, long petiolate leaves and lax, elongate, open inflorescences which are reminiscent of species of *Phytolacca*. The globose fruits dry with a papery pericarp which fractures easily and appears hollow. As the flower buds emerge, the petals increase slightly in length, usually to slightly exceed the sepals, and the filaments elongate pushing the anthers upwards, sometimes included and sometimes exserted from the petals. Plants are reportedly strongly aromatic.

Tovaria pendula is here understood in a broad sense, including a number of plants appearing different in flower dimensions and pubescence. No correlation could be made with the relatively few specimens available, but further study might indicate more than one species is present. Of note is the Gentry collection from Darién which has flowers only about half as big as those from Chiriquí and Peru. Fawcett and Rendle (1914) distinguish *Tovaria diffusa* of Jamaica from *T. pendula* by its sessile fruiting stigmas, narrower sepals and longer petals.

Tovaria pendula ranges from Mexico to Peru and Venezuela. In Panama it is known from middle and upper elevations in Darién and Chiriquí, most collections being from areas of disturbance.

CHIRIQUÍ: Cerro Punta, 7000 ft, *Blum et al. 2415* (MO, SCZ). Between Cerro Punta and Quebrada Iglesia, *Croat 16061* (MO). Near town of San Félix, ca. 13 mi N of Río San Félix bridge, 800–1200 m, *Croat 33502* (MO). N of San Félix 33.4 km from Panamerican Highway, *Mori & Kallunki 6023* (MO). Near Cerro Punta Village, *Webster & Breckon 16568* (MO). DARIÉN: Río Pucuro, 650 m, *Gentry et al. 16858* (MO).

Index of Latin Names

Numbers in **bold face** type refer to descriptions; numbers in roman type refer to synonyms; numbers with daggers (†) refer to names incidentally mentioned.

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FLORA OF PANAMA[1]

BY ROBERT E. WOODSON, JR. AND ROBERT W. SCHERY
AND COLLABORATORS

Part VI

FAMILY 89. RUTACEAE[2]

DUNCAN M. PORTER[3] AND THOMAS S. ELIAS[4]

Trees, *shrubs*, or perennial *herbs*, sometimes scandent or xeromorphic, armed or unarmed; stems, leaves, flowers, and fruits usually punctate glandular, the glands containing aromatic volatile oils. *Leaves* alternate or rarely opposite, 1–3 foliolate or simple, persistent or deciduous; petioles sometimes winged; stipules absent. *Flowers* bisexual and/or unisexual, regular or rarely irregular, hypogynous, usually 3–5-merous, solitary and axillary or in various axillary or terminal, often cymose inflorescences; plants dioecious, monoecious, or polygamous; sepals rarely absent, free or connate, usually imbricate; petals free, rarely connate or absent; stamens as many as the petals and in 1 whorl, or twice as many to numerous and in 2 whorls, the outer whorl often shorter than the inner or occasionally reduced to staminodes, the filaments free or connate, often conspicuously dilated or rarely appendaged basally, the anthers 2(–4)-thecate, versatile, often glandular tipped, introrse, longitudinally dehiscent; intrastaminal disc annular, cupular, or cushionlike, nectariferous, rarely obscure or absent; gynoecium of (1–)2–5(–several) free or variously connate carpels, occasionally rudimentary or absent, the ovary sessile to stipitate, (1–)2–5(–several)-loculed, the ovules 1–2 or more per locule, usually anatropous and epitropous, rarely apotropous, placentation axile or rarely parietal, the styles basal, more or less lateral, or terminal, free, connivent or connate, persistent or deciduous, the stigmas free or connate, simple or lobed. *Fruit* of (1–)2–5(–several) follicles or drupes, or a berry, capsule, samara, or schizocarp; seeds 1 or 2 to several per locule, sessile or funiculate, the endosperm present or absent, the embryo relatively large, straight or curved, the cotyledons plano-convex, sometimes convolute, rarely plicate, the radicle superior.

The Rutaceae includes perhaps 150 genera and 1,500 species widely distributed in the tropical and temperate regions of the world, but most abundant in tropical America, South Africa, and Australia.

Besides the species enumerated below, *Triphasia trifolia* (Burm, f.) P. Wilson, the limeberry, is to be expected as an escape in Panama. This native of south-

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[1] Assisted by National Science Foundation Grant DEB 77-04300 (W. G. D'Arcy, principal investigator).

[2] *Citrus*, *Murraya*, and *Zanthoxylum* by Duncan M. Porter; *Angostura*, *Erythrochiton*, *Esenbeckia*, *Galipea*, *Hortia*, and *Ticorea* by Thomas S. Elias.

[3] Department of Biology, Virginia Polytechnic Institute and State University, Blacksburg, Virginia 24061.

[4] The Cary Arboretum of the New York Botanical Garden, Box AB, Millbrook, New York 12545.

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eastern Asia, widely naturalized in the tropics, is cultivated as an ornamental and hedge plant throughout the tropics and subtropics, including Panama. It is an armed evergreen shrub with 3-foliolate leaves, 3-merous flowers ca. 1 cm in diameter, and a bright red, 1–3 seeded berry ca. 1 mm in diameter.

Literature:

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KEY TO THE GENERA

a. Fruits a fleshy hesperidium, drupe, or drupaceous berry.
  b. Leaves unifoliolate or simple.
    c. Leaves unifoliolate; branches usually armed with axillary spines; stamens 20–60 per flower; fruit a hesperidium ---------- 2. *Citrus*
    cc. Leaves simple; branches unarmed; stamens 5 per flower; fruit a 2-seeded drupe ---------- 6. *Hortia*
  bb. Leaves odd pinnate; branches unarmed; fruit a small berry ---------- 7. *Murraya*
aa. Fruits dry, a capsule, follicle, or samara.
  d. Flowers usually unisexual, rarely bisexual, small; plants usually dioecious ---------- 9. *Zanthoxylum*
  dd. Flowers bisexual, usually large, showy; plants monoclinous.
    e. Fruits capsular, composed of 4 or 5 partially or completely fused carpels.
      f. Flowers small, 1.5–3.5 mm long, inconspicuous, greenish white; fruits large with a small to large hornlike projection on each segment ---------- 4. *Esenbeckia*
      ff. Flowers large, 9–14 cm long, white to cream; fruits small, lacking a hornlike projection on each segment ---------- 5. *Galipea*
    ee. Fruits follicular, composed of individual mericarps, occasionally fused only at the base.
      g. Corolla lobes free or fused only at the base ---------- 1. *Angostura*
      gg. Corolla lobes united into a distinct tube.
        h. Flowers large, 1.5–3.0 cm long, showy, usually brightly colored, usually red to pink; calyx large, 1.0–1.8 cm long; each carpel of the fruit 2-seeded ---------- 3. *Erythrochiton*
        hh. Flowers medium-sized, 8–15 mm long, usually white to cream; calyx small, 3–5 mm long; each carpel of the fruit 1-seeded ---------- 8. *Ticorea*

1. ANGOSTURA

Angostura Roemer & Schultes, Syst. Veg. 4: 188. 1819. TYPE: *Angostura trifoliata* (Willd.) Elias.

Bonplandia Willd., Mem. Acad. Sci. Berlin. 1802: 26–28, *pl. 1804*, non Cavanilles (1800).
Cusparia Humboldt, Essai Geog. Pl. Tabl. Phy. Reg. Equin. 58. 1807. nom. provis.
Conchocarpus Mikan, Delect. Fl. & Faun. Brasil. *tab.* 2. 1820.
Diglottis Nees & Martius, Nova Acta Phys.-Med. Acad. Caes. Leop.-Carol. Nat. Cur. 11: 151, *tab.* 19, *fig. F*; 170, 171, *tab.* 25. 1823.

Trees or *shrubs*, usually with a single stemmed trunk, the branches terete, the branchlets often conspicuously lenticellate. *Leaves* alternate or opposite, 1–7 foliolate, generally clustered near the tips of the branchlets, the leaflets petiolate, the petioles terete, often articulate, the lamina variable, small to large, ovate, obovate, elliptic or oblong. *Inflorescences* usually terminal or upper axillary, racemose,

paniculate, or rarely subcorymbose, the lateral axes generally short, few- to many-flowered, pedunculate. *Flowers* white to cream, bisexual, 4–5-merous, slightly zygomorphic; calyx cupular, campanulate, the lobes distinct to almost indistinguishable, usually acute; corolla united only at the base of the petals, the petals linear to oblong, obtuse to acute at the tip, the petals imbricate in bud, erect to slightly spreading at maturity; stamens 4–5, fertile stamens 2–3, the fertile anthers linear-oblong, erect, longitudinally dehiscent, basifixed, the staminodes linear or lanceolate, inserted at or near the base of the nectary; ovary globose to ovoid, 4–5 carpellate, free but tightly pressed against each other, ovules 1 or 2, superimposed, the ovary surrounded at the base by a cupular nectary, the style filiform, the stigma usually 4–5-ridged. *Fruits* of 1–5 free mericarps, usually obovoid, dehiscing longitudinally from the apex to the base; endocarp free, falling from the mericarp, winged; seed 1 per endocarp, reniform, globose or oblong.

In addition to specimens cited under the species treated here, two collections seem to represent a different species, perhaps new, but definite placement cannot be made without flowers. The two collections are both from the Cerro Jefe area of Panama Province: *Correa & Dressler 1648* (MO); *Dressler 3877* (MO).

1. **Angostura nicaraguiensis** (Standley & L. O. Williams) Elias, comb. nov.—FIG. 1.

Galipea nicaraguiensis Standley & L. O. Williams, Ceiba 3: 206, 207. 1953. TYPE: Between Mt. Esquipulas and Mt. Aleman, Zelaya, Nicaragua, *Shank & Molina 4837* (US).

Shrubs or small *trees* to 8 m high with hard, pinkish wood; branches terete, stout, irregularly sulcate to slightly ridged, light tan to brown, conspicuously lenticellate, the lenticels raised, the branchlets covered with a finely puberulous indumentum, glabrescent. *Leaves* with conduplicate vernation, broadly obovate to broadly obovate elliptic, 20.5–56.0 cm long, 6.5–16.5 cm broad, short acuminate at the apex, attenuate to slightly rounded at the base, with inconspicuous punctations, subcoriaceous to coriaceous, puberulous beneath when young, becoming glabrate, pinnately veined, the veins 12–15 pairs, moderately ascending, weakly anastomosing, conspicuous beneath, the petioles 5.0–8.5 cm long, terete, canaliculate adaxially, stout, striate, expanding at the base, articulated just below the base of the lamina and slightly swollen just above the articulation. *Inflorescence* a narrow panicle 2–4 times longer than broad, terminal or upper axillary; peduncles erect, 2–9 cm long, stout, striate, minutely puberulous, becoming glabrate, usually with conspicuous lenticels; pedicel 3–5 mm long, flaring and merging with the calyx tube. *Flowers* slightly zygomorphic, cream to white; calyx campanulate, 3–4 mm long, glabrous, the lobes ovate, obtuse at the apex, fused near the base, 2–3 mm long, 2.0–2.5 mm broad at the base; corolla lobes fused only at the base, oblong, obtuse apically, slightly tapering at the base, shallowly cucullate, glandular punctate on the inner surface, 11–14 mm long, 3–4 mm broad; stamens zygomorphic, 5, the two functional stamens with laterally fused anthers, the inner thecae often nonfunctional, the anthers 6–8 mm long with a short, rounded mucro at the apex, basifixed with longitudinal dehiscence, the filaments flattened, thicker above, finely puberulous, 3–4 mm long, inserted at

FIGURE 1. *Angostura nicaraguiensis* (Standley & L. Williams) Elias—A. Flowering branch (×½)—B. Flower (×1)—C. Mature leaf (×½)—D. Fruiting inflorescence (×½)—E. Dehiscent capsule (×¾)—F. Endocarp with seed (×¾). [A, B after *Dressler* 8328 (MO): C after *Correa & Dressler* 895 (MO); D, E, F after *Correa & Dressler 611* (MO).]

the base of the disc, the 3 staminodes free, subcylindrical to slightly flattened, finely puberulous, 12–15 mm long; style 1, cylindrical, 2–4 mm long, terminated by a 4–5-furrowed stigma; ovary 5-carpellate, ovules 1 per locule, the placentation axile. *Fruit* of 2–5 mericarps, free, ellipsoid to obovoid with conspicuous transverse ridges, glabrate to finely puberulous, dehiscing initially at the apex, then ventrally and finally dorsally, 18–20 mm long, 12–15 mm wide, attached ventrally near the base; endocarp free, dehiscing from the persistent mericarp, the endocarp flaring after falling from the mericarp, the wings broadly rounded, 10–12 mm long, stramineous, partially enclosing the seed at the base, the basal cup with an oblong to ovate mucra, the mucra 3–4 mm long; seeds orbicular, 5–8 mm in diameter, slightly flattened, smooth, becoming wrinkled upon drying; embryo curved.

Angostura nicaraguiensis is fairly common in eastern Panama, especially along the Atlantic mountain range between 170–700 m altitude, and it should be expected in Colombia in the provinces of Choco and Antioquia.

Although most species of *Angostura* reportedly have 1–3 mericarps per flower, *A. nicaraguiensis* commonly has 3–5 mericarps per flower. Allied with the unifoliolate species, *A. nicaraguiensis* is related to the Brazilian species *A. paniculata* (Engl.) Elias[5] but can be distinguished from it by the much larger leaves.

COLÓN: Santa Rita Ridge lumber road, *Correa & Dressler 611, 673, 895* (all MO); *Croat 34310* (MO); *Duke 15266* (MO), *15267* (MO, NY); *Dwyer 8568* (MO). DARIÉN: Cerro Pirre, *Bristan 1219* (US). Cabecero del Río Pirre, *Bristan 1319* (MO). Cerro Pirre, *Duke 1219* (MO). Between Río Perecenico and Rancho Frio, 170–830 m, *Duke & Elias 13869* (MO, UC). PANAMÁ: La Eneida, along new trail beside López House, region of Cerro Jefe, *Correa & Dressler 713* (MO). 3 mi NE of Altos de Pacora, primary forest, *Croat 22729* (MO). Cerro Jefe, ca. 700 m, *Dressler 3677* (A, MO). 12–17 km N of El Llano, *Dressler 4632* (MO). Cerro Jefe near Río Indio, *Duke 15225* (MO). 5–10 km NE of Altos de Pacora, *Mori & Kallunki 4948* (MO).

2. CITRUS

Citrus L., Sp. Pl. 782. 1753; Gen. Pl. ed. 5, 341. 1754. LECTOTYPE: *C. medica* L. (Wilson, N. Amer. Fl. 25: 221. 1911).

Aromatic glabrous *shrubs* or small *trees*, usually armed with solitary axillary sharp brown-tipped green spines, the branchlets angled, soon terete, green, glandular punctate, the older branches often thornless. *Leaves* alternate, 1-foliolate, persistent; leaflets subcoriaceous, usually thin, glandular punctate throughout, entire to serrate, shiny dark green above, paler and duller beneath; petioles usually more or less winged and articulated with the leaflets. *Flowers* axillary, solitary, paired, or in short corymbose cymes, regular, (4–)5-merous, bisexual or staminate by more or less complete abortion of the gynoecium, 2–5 cm in diameter, often fragrant; plants dioecious or polygamous; calyx shallowly cupular, (4–)5-lobed, persistent; petals (4–)5(–8), free, white, pink, or purplish pink, slightly fleshy, more or less oblong, strongly glandular punctate, imbricate; stamens 20–60, usually 4(6–10) times as many as the petals, polyadelphous or

[5] *Angostura paniculata* (Engl.) Elias, *comb. nov.* basionym: *Cusparia paniculata* Engl. in Mart., Fl. Bras. 12(II): 120. 1874.

free, the filaments linear lanceolate, subulate apically, white, usually variously connate, the anthers oblong to sagittate; intrastaminal disc prominent, annular to cushionlike, supporting the gynoecium; gynoecium syncarpous, the ovary sessile, varying from subglobose and sharply distinct from the much narrower style to truncated, fusiform, or subcylindrical and merging gradually into a style nearly as thick as the upper part of the ovary, glandular punctate, glabrous, (8–)10–14(–18)-loculed, the ovules 4–8 or more per locule in 2 collateral rows, the placentation axile, the style apical on ovary, cylindrical, abruptly expanded into the stigma, deciduous, the stigma more or less capitate, subglobose or oblate spheroidal, sometimes slightly lobed. *Fruit* a berry (hesperidium), ellipsoidal and often mammillate apically, or pyriform to globose and sometimes depressed apically, the pericarp differentiated into a coriaceous glandular-punctate exocarp (the skin) green to red orange at maturity and dotted with numerous oil glands, a thick spongy white mesocarp (the rind), and a membranaceous endocarp filled with stalked fusiform pulp vescicles containing a watery acid to sweet tissue (the pulp), the thin membranous radial locule walls often loosely coherent and easily separated from one another as well as from the spongy white fruit axis; seeds ellipsoidal to obovoid, plump or flattened, more or less angular, sometimes beaked apically, usually several per locule at the inner angle, the testa coriaceous, the endosperm absent, the embryos 1–many, white or green, the cotyledons fleshy, plano convex, often unequal.

A genus of southern and southeastern Asia and Malaysia that is widely cultivated in all warmer areas of the world. Swingle and Reece (1967) ascribe 16 species to *Citrus*, while Tanaka (1954) lists 145 species for the genus. Specific distinctions are complicated not only by hybridization within the genus and with closely related genera, but also by such phenomena as nucellar polyembryony with rejuvenation by nucellar progeny of more or less senescent varieties long propagated asexually, and the spontaneous production of autotetraploids (see Swingle and Reece, *op. cit.*, pp. 359–369, for a discussion of the problems inherent in determining specific limitations in the genus). Failure to take such processes into account has led Tanaka to recognize an overabundance of species in *Citrus*. The number recognized by Swingle and Reece is a much closer reflection of the actual situation in the genus.

Many species have escaped from cultivation and become naturalized. A complication is added where a species is cultivated and later abandoned to become part of the second growth vegetation. Here the presence of a solitary tree in the forest may or may not indicate naturalization. Such is the case in Panama, where only *Citrus aurantifolia* (Christm.) Swingle unquestionably is naturalized.

Another complication in the lowland tropics is that fruit color cannot reliably be used for identification. Whereas elsewhere this can be a useful and reliable character, here fruits often remain green at maturity. Fruit morphology and taste are the most important field characters for positive identification, as many species are difficult to separate vegetatively.

Besides the species discussed below, the following also are to be expected

in Panama: *C. limetta* Risso (the sweet line); *C. medica* L. (the citron); and *C. paradisi* Macfad. (the grapefruit).

Literature:

Purseglove, J. W. 1968. Tropical Crops. Dicotyledons 2. pp. 495–522. London.
Swingle, W. T. & P. C. Reece. 1967. The botany of *Citrus* and its wild relatives. Pp. 190–430 *in* W. Reuther et al. (Editors), The Citrus Industry. Vol. 1. History, World Distribution, Botany, and Varieties. Rev. ed. Berkeley.
Standley, P. C. 1928. Rutaceae, *in* Flora of the Panama Canal Zone. Contr. U.S. Nat. Herb. 27: 222–223.
Tanaka, T. 1954. Species problem in *Citrus*. Tokyo.

a. Petioles broadly winged, the wings oblanceolate to apically broadened, 2–32 mm wide.
  b. Wings oblanceolate, 2–9 mm wide; branchlets usually with numerous axillary spines 5–17 mm long; mature fruits ellipsoidal, mammillate apically, green to yellow, the core solid ——— 1. *C. aurantifolia*
  bb. Wings broadened apically, mostly 1–3 cm wide; branchlets spineless, or axillary spines 5 mm long or less; fruits depressed or flattened apically.
    c. Wings mostly 1.0–1.5 cm wide; branchlets usually spineless; mature fruits globose, orange to red, the core hollow ——— 2. *C. aurantium*
    cc. Wings mostly 2–3 cm wide; branchlets with axillary spines 2–3 mm long; mature fruits subglobose, oblate spheroidal, or subpyriform, green to yellow, pink, or red, the core solid ——— 3. *C. grandis*
aa. Petioles narrowly winged or margined, the wings 2 mm wide or less.
  d. Branchlets usually spineless; mature fruits depressed globose, green to red, the peel easily separating from the segments ——— 5. *C. reticulata*
  dd. Branchlets usually with at least a few axillary spines; mature fruits globose or ovoid, green to yellow or orange, the peel not easily separating from the segments.
    e. Petioles winged; axillary spines few, 5 mm long or less; mature fruits globose, flattened or depressed apically, yellow green to orange, sweet ——— 6. *C. sinensis*
    ee. Petioles margined; axillary spines usually many, to 27 mm long; mature fruits ovoid, mammillate apically, light yellow, acid ——— 4. *C. limon*

1. **Citrus aurantifolia** (Christm.) Swingle, J. Wash. Acad. Sci. 3: 465. 1913.

Limonia aurantifolia Christm. in L., Pflanzensyst. 1: 618. 1777. TYPE: Figure in *Rumphius*, Herb. Amboin. 2: *pl.* 29. 1741.

Shrubs or *trees*, 2–8 m high, usually armed with numerous axillary spines 5–17 mm long. *Leaflets* oblong elliptic to ovate, acute to obtuse and abruptly acuminate and somewhat emarginate apically, rounded basally, the margins crenulate and somewhat revolute, 37–134 mm long, 17–62 mm wide; petioles oblanceolate winged, 5–28 mm long, 2–9 mm wide, articulated with the leaflet. *Flowers* with the peduncles 3–5 mm long; calyx shallowly 4–5 lobed, fleshy, puberulent, glandular punctate, ca. 2 mm high, the lobes broadly triangular, to 1 mm long; petals 4–5, white, oblong lanceolate, 11–14 mm long, ca. 4 mm wide; stamens 20–25, the filaments 4–6 mm long, connate into a number of groups, the anthers linear sagittate, 2–3 mm long; intrastaminal disc fleshy, ca. 1 mm high; ovary obovoid, depressed at the base of the style and sharply distinct from it, 2–3 mm high, the style 2–3 mm long, soon deciduous, the stigma subglobose, depressed apically, ca. 2 mm in diameter. *Fruits* ellipsoidal, mammillate apically, green to yellow, 3.5–6.0 cm in diameter, acid, the core solid.

The lime apparently is native to Assam, Burma, Thailand, and Malaysia. *Citrus aurantifolia* was introduced into the New World by Columbus in 1493. It is cultivated throughout Panama, and is commonly known as *limón* or *limón verde*. It escapes and is naturalized.

CANAL ZONE: Barro Colorado Island, *Croat 9190* (MO). Coastline between Garotte and La Guaira, *D'Arcy 9375* (MO). Boy Scout Road, Madden Dam area, *Porter et al. 4023* (MO). Barro Colorado Island, *Shattuck 88, 89* (both MO). Cultivated, Balboa, *Standley 25668* (F, MO, US). Mt. Hope Cemetery, *Standley 28835* (US). Between France Field and Cativa, Colón, *Standley 30226* (US). Obispo, *Standley 31760* (US). DARIÉN: Near El Real along road to Pinogana, *Croat & Porter 15480* (MO). PANAMÁ: Punta Paitilla, *Standley 26307* (US). Río Tocumen, *Standley 29334* (US).

2. **Citrus aurantium** L., Sp. Pl. 782. 1753. TYPE: (LINN, not seen).

Trees, 5–6 m high, unarmed, or the few axillary spines 5 mm long or less. *Leaflets* broadly elliptic to obovate, often abruptly or obtusely acuminate and somewhat emarginate apically, narrowed to a cuneate base, the margins crenulate and somewhat revolute, 58–118 mm long, 32–75 mm wide; petioles broadly winged apically, 14–27 mm long, mostly 10–15 mm wide, but sometimes narrower, narrowing to an almost wingless base, articulated with the leaflet. *Flowers* solitary, the peduncles puberulent, 9–11 mm long in fruit; calyx 5-lobed, puberulent, the lobes obtuse, ca. 2 mm long. *Fruits* at maturity globose, depressed or flattened apically, orange to red, 4–6 cm in diameter, acid, the core hollow.

The sour orange apparently is native to Assam, Burma, and adjacent southwestern China.

The following sterile specimen also probably represents this taxon: Darién: "Cuipo forests near Santa Fé. Aromatic unarmed tree in undisturbed forest." *Duke 12270* (MO, OS). According to Standley (1928), this species "is occasionally found wild about the [Canal] zone." However, specimens determined by him as *Citrus aurantium* have proved on examination to be *C. aurantifolium*.

Citrus aurantium was introduced into the New World by Columbus in 1493. It does not appear to be cultivated widely in Panama. It is commonly known as *naranja ácida* or *naranja agria*.

BOCAS DEL TORO: Finca 4 (Delta) 10 mi NW of Almirante, *D'Arcy 11192* (MO). CANAL ZONE: Barro Colorado Island, *Croat 9184, 9197, 14944, 14945, 34373* (all MO). CHIRIQUÍ: Old citrus grove, S side of El Hato del Volcán, *Nee 14148* (MO). DARIÉN: Near Santa Fé, *Duke 12270* (MO, OS). PANAMÁ: San Jose Island, beach at mouth of Río Mato Puerco, *Erlanson 474* (GH, US).

3. **Citrus grandis** (L.) Osbeck, Dagbok Ofwer Ostin. Resa 98. 1757. TYPE: China, *Osbeck* (S not seen).

Trees armed with axillary spines 2–3 mm long. *Leaflets* oval, retuse apically, obtuse basally, the margins crenate and somewhat revolute, to 95 mm long, 72 mm wide; petioles broadly winged, wedge shaped, truncate apically, obtuse basally, to 32 mm wide, 40 mm long, articulated with the leaflet. *Flowers* borne singly, in axillary clusters, or in subterminal inflorescences; calyx 5-lobed; petals 5; stamens 20–25, the anthers linear; ovary globose, sharply delimited from the

deciduous style. *Fruits* at maturity subglobose, oblate spheroidal, or subpyriform, depressed or flattened apically, green to yellow, pink, or red, 11–17 cm in diameter, acid, the peel thick, the core solid.

Flower and fruit characteristics in the above description are from Swingle and Reece (1967).

The pummelo apparently is native to the East Indian region. *Citrus grandis* was introduced into the New World via the West Indies in the Seventeenth Century.

CANAL ZONE: Cultivated, Barro Colorado Island, *Croat 4210* (MO).

4. **Citrus limon** (L.) Burm. f., Fl. Ind. 173. 1768.

Citrus medica var. *limon* L., Sp. Pl. 782. 1753. TYPE: (LINN, not seen).

Small *trees* to ca. 6 m high, heavily armed with numerous axillary spines 5–27 mm long. *Leaflets* elliptic to oval, obtuse to retuse and abruptly acuminate apically, broadly cuneate basally, the margins crenulate and somewhat revolute, 43–115 mm long, 17–60 mm wide; petioles narrowly margined, but not winged, 5–7 mm long, ca. 1 mm wide, articulated with the leaflet. *Flowers* not seen in the Panamanian specimen. *Fruits* at maturity ovoid, mammillate apically, light yellow, 5–10 cm long, acid, the peel not easily separating from the segments.

The lemon apparently is native to northeastern India, northern Burma, and southern China. *Citrus limon* was introduced into the New World by Columbus in 1498. It is grown commercially in Chiriqui.

CANAL ZONE: Cultivated, Barro Colorado Island, *Croat 10134, 10767* (both MO); *Shattuck 86, 719* (both MO).

5. **Citrus reticulata** Blanco, Fl. Filip. 610. 1837. NEOTYPE: Philippines, *Luzon & Merrill*, Species Blancoanae No. 402 (not seen), (Swingle & Reece, 1967, p. 380).—FIG. 2.

Trees to 8 m high, unarmed. *Leaflets* oblong elliptic to ovate or obovate, retuse apically, cuneate basally, the margins crenulate and somewhat revolute, 37–72 mm long, 24–48 mm wide; petioles usually slightly winged apically, 6–14 mm long, to 2 mm wide, articulated with the leaflet. *Flowers* with the peduncles 3–4 mm long; calyx 5-lobed, glandular punctate, ca. 3 mm in diameter, the lobes obtuse, ciliate, ca. 1 mm long; petals 5, white, oblanceolate to oblong, 7–8 mm long, 2–4 mm wide; stamens ca. 20, the filaments connate into several groups, the anthers sagittate; ovary depressed globose, 2 mm in diameter, the style columnar, 3 mm long, the stigma globose, 2 mm in diameter. *Fruits* depressed globose, green to red, 5–8 cm in diameter, sweet, the peel easily separating from the segments.

Citrus reticulata, the tangerine or mandarin orange, apparently is native to Indo-China. It was not introduced into the New World until the 19th century. It is grown commercially in Chiriqui.

CANAL ZONE: Cultivated, Barro Colorado Island, *Croat 4566, 7014, 8892, 9401, 14579,*

FIGURE 2. *Citrus reticulata* Blanco—A. Habit (×⅔).—B. Flower (×3¼). [After *Lewis et al. 1807* (MO)].

14870, 16567 (all MO). COCLÉ: Hills NE of El Valle de Antón, 2000 ft, *Lewis et al. 1807* (MO).

6. **Citrus sinensis** (L.) Osbeck, Reise Ostind. China 250. 1765.

Citrus aurantium var. *sinensis* L., Sp. Pl. 783. 1753. TYPE: Bauhin (BAS, not seen).

Shrubs or *trees* to 8 m high, the few axillary spines 2–3 mm long. *Leaflets* oblong elliptic to ovate or obovate, acute or obtuse and retuse apically, cuneate basally, the margins crenulate and somewhat revolute, 33–90 mm long, 15–43 mm wide; petioles usually with a narrow oblanceolate wing, 6–18 mm long, 1–2 mm wide, articulated with the leaflet. *Flowers* solitary, the peduncles glabrous, 7–12 mm long in fruit; calyx 5-lobed, 6 mm in diameter, the lobes acute, ciliate, 2 mm long. *Fruits* at maturity globose, flattened or depressed apically, yellow green to orange, 4–12 cm in diameter, sweet, the peel not easily separating from the segments.

The sweet orange apparently is native to northern Burma, southeastern China, and Indo-China.

Citrus sinensis was introduced into the New World by Columbus in 1493. It is grown commercially in Chiriqui, and is commonly known as *naranja*.

CANAL ZONE: Cultivated, Barro Colorado Island, *Croat 6002, 10765, 10766* (all MO). DARIÉN: 2–3 mi SE of El Real, *Duke 4861* (MO).

3. ERYTHROCHITON

Erythrochiton Nees & Mart., Nova Acta Acad. Leop.-Carol. 11: 151, 165. *tab. 18.* 1823. TYPE: *E. brasiliensis* Nees & Mart.

Shrubs or small *trees* with terete, light to dark brown branches. *Leaves* simple or unifoliolate, opposite or spirally arranged, petiolate, small to very large, chartaceous to leathery, elliptic, lanceolate to oblanceolate, acute to acuminate, entire, glandular dotted, usually glabrous. *Inflorescences* terminal or axillary, corymbose, cymose, or paniculate, with a short to long peduncle. *Flowers* large, often showy, bisexual, 5-merous; calyx large, the lobes united only at the base, sometimes unequally 5-cleft, persisting into fruit; corolla gamopetalous, apparently zygomorphic, the corolla tube straight or curved, cylindric, almost equaling to slightly exceeding the calyx lobes, the lobes unequal, spreading, pink to red; stamens 5, all fertile or 2–3 sterile, the filaments adnate to the corolla tube, anthers lanceolate to oblong linear, erect; ovary globose, 5-carpellate, ovules 2, collateral or superposed, the ovary enclosed in an annular disc, the style filiform, the stigma capitate or 5-lobed. *Capsules* 5-locular, the carpels connate only at the base, the individual carpels oblong, rounded at the apex, 2-valved; endocarp elastic and becoming cartilaginous; bivalvate, light straw colored; seeds 2 per carpel, angular, usually oblong; embryo curved with little endosperm.

Erythrochiton is a small genus, primarily shrubby, of perhaps 4 or 5 species in New World tropical regions. Two species are found in the lowland forest, especially along streams, of western Panama.

a. Inflorescences 1–3-flowered, short pedunculate, the peduncles 1.2–3.5 cm long; corolla sparsely pilose ..... 1. *E. incomparabilis*
aa. Inflorescences 6–8-flowered, long pedunculate, the peduncles 8–18 cm long; corolla densely sericeous ..... 2. *E. lindeni*

1. **Erythrochiton incomparabilis** Riley, Bull. Misc. Inform. 1927: 121. 1927. TYPE: Panama, *Collenette 470* (K, not seen; isotype, MO).—FIG. 3.

Shrubs or small *trees*, 1–5 m high; branches terete, light to dark brown, glabrous, inconspicuously lenticellate. *Leaves* opposite, simple, usually clustered near the tips of the branches, narrowly or broadly elliptic to obovate, 16–24 cm long, 6–11 cm broad, attenuate at the base and acuminate to long acuminate at the apex, chartaceous to slightly coriaceous, gland dotted with numerous tiny glands, glabrous, pinnately veined, the lateral veins usually 9–12 pairs, gradually ascending, prominent beneath; petiole stout, canaliculate adaxially, narrowly winged, 5–10 mm long. *Inflorescences* terminal, corymbiform, 1–3 flowered, pedunculate, the peduncles 1.2–3.5 cm long, erect, glabrous, bracteate, the bracts ovate, 8–15 mm long, 3–6 mm wide, short acuminate at the tip. *Flowers* showy; pedicellate, the pedicels 0.8–1.6 cm long, glabrous; calyx ellipsoid, the lobes fused at the base, elliptic, 1.0–1.8 cm long, 0.7–1.0 cm wide, erect, gland dotted, red, persisting and enclosing the fruits; corolla pink, zygomorphic, the tube 1.8–2.5 cm long, sparsely pilose, the lobes spreading, 4 dorsal and 1 ventral, 2.0–2.5 cm long, 3–6 mm broad, rounded at the tip, conspicuously gland dotted; stamens 5,

FIGURE 3. *Erythrochiton incomparabilis* Riley—A. Flowering branch (×½)—B. Flower (×1)—C. Fruiting inflorescence (×½)—D. Dehiscent capsule (×½)—E. Endocarp with seed (×1). [A, B after *Dressler 5215* (MO); C, D, E after *Mori & Kallunki 4764* (MO).]

inserted on the corolla tube, the filaments filiform, 0.8–1.0 cm long, the anthers not seen; ovary 4–5 locular, the style cylindric, 2.4–3.0 cm long, the stigma capitate, the ovary surrounded by an annular nectary. *Capsules* of 4 or 5 carpels united only at the base, each carpel oblong, 1.0–1.4 cm long, 5–7 mm wide, rounded at the apex, obliquely striate on the sides, dark brown; endocarp elastic but becoming brittle upon drying, bivalvate at maturity, usually 2 seeded; seeds rounded or nearly so, 3–5 mm long, slightly tuberculate, dark brown.

VERAGUAS: Coiba Island, *Collenette 470* (MO). Río Primero Braso, near Santa Fé, *Croat 25470* (MO). Río Santa María, 8 km NW of Santa Fé, *Dressler 5215* (NY). Road to Calovébora, 10 km NW of Santa Fé, *Mori & Bolten 7646* (MO). 2.6–2.7 km from Escula Agricola Alto de Piedra, NW of Santa Fé, *Mori & Kallunki 4764, 5345* (both MO).

2. **Erythrochiton lindeni** (Baill.) Hemsl., Biol. Centr. Am. Bot. 1: 166, 167. 1879.

Toxosiphon lindeni Baill., Adansonia 10: 312. 1872. TYPE: not seen.

Shrubs or small *trees* to 4 m high; branches stout, terete, becoming dark brown with age, glabrous, with oblong to narrowly elliptic lenticels. *Leaves* opposite, clustered near the tip of the branches, unifoliolate; lamina broadly elliptic to obovate, 17.5–30.0 cm long, 6.3–14.0 cm wide, short acuminate at the tip, tapering to a cuneate base, chartaceous to subcoriaceous, glandular punctate on both the surfaces, glabrous, pinnately veined, the veins 10–14 pairs, ascending, anastomosing; petiole terete, glabrous, slightly striate, 4.3–8.2 cm long. *Inflorescences* terminal, 2–4 branched small cymes, the peduncles erect, 8–18 cm long, striate, glabrous, bracteate, bracts not seen; pedicels 6–8 mm long. *Flowers* showy, creamy white, 5-merous; calyx lobes free, narrowly lanceolate, 1.0–1.6 cm long, erect, inconspicuously gland dotted, persistent in fruit; corolla to 4 cm long, arcuate, densely sericeous, the corolla tube 2.5–3.0 cm long, the lobes oblong to ovate, 1.0–1.2 cm long, spreading; stamens (not seen) 5, included; ovary not seen, the style filiform, the stigma appearing capitate. *Capsules* (fide Baillon) of 5 free carpels ca. 2.5 cm long, oblong, laterally compressed, dorsally carinate; endocarp elastic, bivalved; seeds subreniform.

This rare, showy-flowered shrub is native to Central America, ranging from southern Mexico to Panama.

BOCAS DEL TORO: Changuinola, forest near Luzon, *Kennedy 3252* (MO).

4. ESENBECKIA

Esenbeckia H.B.K., Nov. Gen. Sp. Pl. 7: 246. 1825. TYPE: *E. pilocarpoides* H.B.K.

Polembryum A. Juss., Mem. Mus. Paris 12: 519. 1825.

Small to medium sized resinous *trees* or *shrubs* with thin, light colored bark separating in flat, irregular plates. *Leaves* alternate, pseudopposite to rarely opposite, simple, or 1–5 foliolate, the leaflets variable, chartaceous to subcoriaceous, pellucid-punctate, petiolate, glabrous to variously pubescent. *Inflorescences* terminal or upper axillary, paniculate, few to many flowered, often

subglomerate, pedunculate. *Flowers* small, greenish white, bisexual, (4–)5-merous, regular; calyx cupular, the lobes ovate, obtuse at the apex, imbricate in bud; stamens 5, free, all fertile, inserted at the base of the nectary, the filaments filiform, the anthers tiny, subcordate at the base; ovary globose, depressed on the top, 5-lobed, frequently covered with numerous tubercules, 5-locular, ovules 2 per locule, superimposed, the style filiform, the stigma 1 or 5 lobed. *Capsules* dry, capsular, subglobose to obovoid, composed of 5 carpids, each carpid with a small to conspicuous hornlike projection; seeds oblong to reniform, 1–2 per locule, the testa smooth to rugose.

Esenbeckia is a New World genus of perhaps 20 species extending from Texas and Mexico throughout Middle America to central South America. Three species are known from Panama.

a. Leaves trifoliolate, alternate.
   b. Trees 10–20 m tall; petioles 5.5–8.5 cm long; leaflets 10.0–20.5 cm long; capsules urceolate, each segment conspicuously beaked ..... 1. *E. alata*
   bb. Shrubs to 5 m tall; petioles 1.0–3.5 cm long; leaflets 5–12 cm long; capsules subglobose, the segments not beaked ..... 2. *E. litoralis*
aa. Leaves simple, opposite or ternate ..... 3. *E. panamensis*

1. **Esenbeckia alata** (Karst. & Triana) Triana & Planchon, Ann. Sci. Nat. Bot. 14: 306. 1872.

Kuala alata Karst. & Triana, Linnaea 28: 428–429. 1856. TYPE: not seen.

Trees, 10–20 m high; branches terete, glabrous, light to dark brown, inconspicuously lenticellate. *Leaves* alternate, trifoliolate, petiolate, the petioles terete, becoming canaliculate adaxially on the apical ½ of the petiole, (3–)5.5–8.5 cm long, with fine appressed trichomes; leaflets elliptic to slightly obovate, 10.0–20.5 cm long, 5.0–8.2 cm wide, short acuminate at the apex and tapering to a cuneate base, chartaceous with numerous tiny glands on both the surfaces, glabrous, pinnately veined, the veins 14–18 pairs, moderately ascending, anastomosing. *Inflorescence* a narrow panicle 2–3 times longer than broad, terminal; peduncles 6–8 cm long, striate, finely puberulent, bracteate, the bracts ovate, acute, 0.5–1.0 mm long. *Flowers* (Colombian material) tiny, inconspicuous, 5-merous; buds globose, 1.8–2.2 mm long; calyx lobes imbricate, broadly ovate, acute at the tip, densely hairy, 0.7–1.0 mm long; corolla lobes slightly imbricate, the lobes oblong to elliptic, 1.8–2.0 mm long, 1.0–1.5 mm wide, obtuse at the tip, pellucid punctate; stamens erect, the filaments somewhat flattened, 1.8–2.2 mm long, the anthers 0.2–0.4 mm long, cordate, lobed to the middle; ovary enclosed in a multi-lobed disc, the ovary composed of 5 carpels, the ovules 2 per carpel, the style 1, narrowly cylindric, 1.5–2.0 mm long, the stigma 1, terminal, spatulate. *Capsules* 5-locular, urceolate, flattened on the apex, 1.9–2.5 cm high, 2.5–3.1 cm across, to 5 cm across following dehiscence, coriaceous, becoming indurate at maturity, each segment conspicuously beaked near the apex, the beak large, stout, to 1.2 cm long, sometimes with a smaller, secondary beak located at midway to near the base of each segment; endocarp cartilaginous, 2-winged, the wings oblong, spreading, rounded at the tip, partly enclosing the seed at the base; seed ovoid, 10–12 mm long, oblique at the base, obtuse to acute at the tip, flattened on 1 side, drying shiny brown.

This small to medium sized tree also occurs in northern South America. The leaves and fruits are glandular and emit a strong resinous odor when bruised or crushed.

LOS SANTOS: Tonosí along Quebrada Ocho Paso, *Stern et al. 1822* (MO, US). PANAMÁ: Television tower on ridge 3 km S of Alcalde Díaz, *Nee 8570* (MO).

2. **Esenbeckia litoralis** Donnell Smith, Bot. Gaz. 23: 242. 1897. TYPE: not seen.

Shrubs, medium to large sized, to 5 m high; branches terete, yellowish brown and conspicuously lenticellate, the lenticels slightly raised, whitish, the young branchlets densely villous. *Leaves* alternate, trifoliolate, petiolate, the petioles terete, canaliculate adaxially, 1.0–3.5 cm long, densely villous; terminal leaflet elliptic to obovate, 5–12 cm long, 3–7 cm wide, the lateral leaflets ½–⅓ as large as the terminal leaflet, subacute to rounded at the apex, tapering at the base, sessile, glabrous above, villous beneath, especially on the midvein, chartaceous, the lateral veins 10–14 pairs, moderately ascending, conspicuous beneath. *Inflorescenses* terminal, racemiform, 3.5–5.0 cm long, bracteate, the bracts ovate, 2–3 cm long. *Flowers* (fide Donnell Smith, not seen in Panamanian material) 5-merous, subglomerate; calyx lobes imbricate, semiorbicular, 2–3 mm long; corolla lobes imbricate in bud, the lobes oblong, 3.0–3.5 mm long, obtuse at the apex, sparingly and minutely pellucid-punctate; stamens equaling the petals, the filaments dilated below, the anthers cordate and lobed to the middle; ovary enclosed in a 10-lobed, cup shaped disc, the ovary composed of 5 carpels each furnished with 3–5 yellow, glandlike warts, the ovules 2 per carpel; style subulate, ca. 1 mm long. *Capsules* 5-locular, subglobose, coriaceous, deeply 5-lobed, 2.5–3.5 cm broad, not beaked; endocarp cartilaginous, 2-winged, the wings oblong and curving outward at the apex, partially enclosing the seed at the base; seed ovoid to obovoid, 10–12 mm long, slightly compressed, drying dark brown.

PANAMÁ: Bejuco, *Allen 982* (MO, US).

3. **Esenbeckia panamensis** Elias.[6] TYPE: Panama: *D'Arcy & D'Arcy 6126* (MO, holotype).—FIG. 4.

Shrubs or small *trees*, 2–5 m high; branches terete, glabrous, grayish brown with scattered, inconspicuous elliptic lenticels. *Leaves* opposite or ternate, short petiolate, the petioles terete, canaliculate and narrowly winged adaxially, 6–12 mm long, glabrous; lamina elliptic, 16.5–30.0 cm long, 6.3–12.7 cm wide, short to long acuminate at the tip, tapering to a cuneate base, chartaceous to slightly coriaceous with numerous tiny glands on both the surfaces, glabrous, pinnately veined, the veins 9–12 pairs, spreading, anastomosing. *Inflorescence* a reduced, few-flowered panicle, terminal, pedunculate, the peduncle 0.6–2.5 cm long, finely striate, bracteate, the bracts ovate, acute, 2–4 mm long. *Flowers* small,

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[6] *Esenbeckia panamensis* Elias, sp. nov. Frutex vel arbor ad 5 m alta. Habitat et textura *E. pilocarpoides* sed differt folia simplicia. Folia opposita aut ternata, elliptica, 16.5–30.0 cm longa, 6–12 mm longa petiolata. Inflorescentiae terminales, adscendentes, paucifloridae, breviter paniculatae. Flores 6–9 mm longa, virides. Capsula 1.4–2.0 cm longa, urniformes, 5-partita, segmentis cornutis.

FIGURE 4. *Esenbeckia panamensis* Elias—A. Fruiting branch (×½).—B. Flowering branch (×½).—C. Dehiscent capsule (×½).—D. Endocarp with seed (×2½). [A, C, D after *Duke* 6553 (MO); B after *D'Arcy & D'Arcy 6126* (MO).]

inconspicuous, green, 5-merous; buds globose, 1.5–2.2 mm long; calyx lobes imbricate, broadly ovate, acute to rounded at the tip, densely hairy, 1.0–1.5 mm long; corolla lobes imbricate, the lobes ovate, 6–9 mm long, 2.5–3.5 mm wide, acute at the apex, conspicuously pellucid-punctate on the outer surface of the lobes; stamens erect, the filament 1.5–2.0 mm long, the anthers 0.3–0.4 mm long, cordate, lobed at the base to near the middle; ovary enclosed in the multilobed disc, composed of 5 carpels; style 1, cylindric, 1.5–2.0 mm long; stigma 1, capitate. *Capsules* 5-locular, urceolate, flattened on the top, 1.4–2.0 cm high, 2.0–2.5 cm across at the apex, coriaceous, becoming indurate at maturity, each segment beaked, the beak stout, spreading to slightly recurved, 3–7 mm long; endocarp cartilaginous, light straw colored, 2-winged, the lobes oblong, spreading and rounded at the apex, partly enclosing the seed at the base; seed ovoid to ellipsoid, 9–11 mm long, slightly hooked at the apex, dark brown.

Superficially, this new species resembles *Esenbeckia pilocarpoides* H.B.K. of northern South America; however, it has unifoliolate leaves while *E. panamensis* bears only simple leaves. In addition, the Panamanian species has a reduced inflorescence. It occurs in eastern Panama and adjacent portions of Colombia (Choco: Alto Guillermo, over Río Arquia behind Sautata, *Duke 15390* [MO]).

COLÓN: Santa Rita Ridge E of Transisthmian Highway, *Gentry 6581* (MO). Road into Santa Rita, E of Aqua Clara rain gauge, *Kennedy 2743* (MO). DARIÉN: Razorback ridge on Cerro Pirre, *Duke 6553* (MO). Slopes of Cerro Pirre, 500–1000 m, *Gentry & Clewell 7121* (MO); *Mori & Kallunki 5438* (MO).

5. GALIPEA

Galipea Aublet, Hist. Pl. Gui. Franc. 2: 662, *tab.* 269. 1775. TYPE: *G. trifoliata* Aublet.

Endostephium Turcz., Bull. Soc. Nat. Moscou. 36(2): 227. 1823.
Costa Vellozo, Fl. Flum. 19. 1825.
Systemon Regel, Ind. Sem. Hort. Petrop. 38. 1856.

Trees or *shrubs*, the branches often conspicuously lenticellate. *Leaves* alternate, (1–)3-foliolate, the lamina elliptic to obovate, membranous to coriaceous, pellucid punctate, usually glabrous, the petiole often short, semiterete, usually narrowly winged. *Inflorescences* terminal and axillary, corymbose to paniculate, few to many flowered, the peduncles often long. *Flowers* fragrant, often showy, bisexual, 5-merous; calyx short campanulate to tubular, the lobes rarely distinct, erect, usually acute at the apex; corolla connate, several to many times longer than the calyx, the tube straight to slightly arcuate, cylindric, often narrowly so, the lobes imbricate in aestivation; stamens 5 to 8, fertile stamens usually 2, fertile anthers introrse, erect, longitudinally dehiscent, basifixed, staminodea linear, the filaments united in a tube coherent with the corolla tube; ovary usually globose to ellipsoid, subtended and partially enclosed in a cupular nectary, 4–5 carpellate, ovules 2, collateral, one slightly superposed, the style filiform, the stigma 3–5 lobed. *Capsules* 5-locular, oblong to subglobose, the individual segments connate basally, carinate, endocarp usually cartilaginous, bivalvate; seeds laterally com-

pressed; embryo curved to uncinate with little or no albumen, radicle retracted between the cotylendons.

Galipea includes eight to ten species centered in northern South America with two species known from eastern Panama. One South American species, *Galipea jasminiflora*, has been incorrectly reported from Panama, but the Panamanian specimens assigned to this name are properly identified as *G. trifoliata*.

Literature:

Elias, T. S. 1970. Notes on the genus *Galipea* (Rutaceae) in Central America. J. Arnold Arbor. 51: 427–430.

a. Leaves trifoliolate; corolla tube slender, 9–11 mm long, the lobes oblong to narrowly obovate, 4–5 mm long, obtuse at the apex ..... 2. *G. trifoliata*
aa. Leaves unifoliolate; corolla tube stout, 1.1–1.4 cm long, the lobes narrowly obovate, 1.3–1.6 cm long, acute at the apex ..... 1. *G. panamensis*

1. **Galipea panamensis** Elias, J. Arnold Arbor. 51: 428–430. 1970. TYPE: Panama, *Dressler 3682* (A, holotype; MO, isotype).—Fig. 5.

Trees to 7 m high; branches terete, slightly sulcate, grayish to light brown, glabrous, lenticellate, the lenticels slightly elevated. *Leaves* 1-foliolate, 11–21 cm long, 3.0–9.2 cm broad, coriaceous, elliptic to narrowly elliptic, attenuate at the base, acuminate at the apex, pellucid punctate, glabrous, the lateral veins 5–11 pairs, prominent beneath; petiole slightly winged above, swollen and becoming woody at the base, articulated near the base of the lamina, 9–16 mm long. *Inflorescences* terminal and axillary; corymbs congested, 12–22 flowered; peduncles erect to semi-erect, conspicuously lenticellate, 1.2–3.5 cm long. *Flowers* white; calyx campanulate, pellucid punctate, puberulous, 3–4 mm long, the lobes transversely ovate, the apex acute, minutely ciliate, 0.5–1.0 mm long; corolla puberulous, conspicuously pellucid punctate, 2.3–3.0 cm long; tube cylindrical, arcuate in bud, 1.1–1.4 cm long, the lobes imbricate in aestivation, narrowly obovate, the apex acute, dilated to slightly recurved, 1.3–1.6 cm long, to 3.5 mm wide; stamens 6–7, included, inserted near the apex of the tube, the filaments short, to 1 mm long, fertile anthers 2, 4–6 mm long, basifixed, longitudinally dehiscent; staminodea free, complanate, 6–8 mm long; ovary 5-carpellate, the style cylindrical, 10–12 mm long; stigma 5, oblong, 1–2 mm long. *Capsules* 5-locular, subglobose, 1.0–1.5 cm long, the cocci basally connate, carinate, dehiscing from the apex to near the middle; endocarp cartilagenous, bivalvate, 1-seeded, basally fused, the wings obtuse at the apex; seeds orbicular to obovoid, slightly compressed laterally, pubescent.

Restricted to eastern Panama, *Galipea panamensis* has conspicuous white, fragrant flowers. The corymbose inflorescence readily distinguishes this species from others in the genus in which the inflorescence is narrowly paniculate.

COLÓN: Santa Rita Ridge lumber road, E of Colón, *Correa & Dressler 766* (MO); *Dressler 3659* (A, MO). DARIÉN: Parallel to Río Tucutí on ridge upstream from Tucutí, *Duke 5264* (MO). Loma Cuasí, behind Manené, *Duke 13607* (MO). PANAMÁ: Cerro Jefe, ca. 700 m, *Dressler 3682* (A, MO). Cerro Jefe near Río Indio, *Duke 15224* (MO).

FIGURE 5. *Galipea panamensis* Elias—A. Flowering branch (×½)—B. Flower and bud (×1).—C. Fruiting branch (×½).—D. Dehiscent capsule (×1).—E. Endocarp with seed (×1). [A, B after *Duke 5264* (MO); C, D, E after *Correa & Dressler 766* (MO).]

2. **Galipea trifoliata** Aubl., Hist. Pl. Gui. Franc. 2: 662, *tab.* 269. 1775. TYPE: not seen.

Trees to 6 m high; branches terete, irregularly sulcate, brown to reddish brown, glabrescent, conspicuously lenticellate, the lenticels light tan. *Leaves* trifoliolate, petiolate, the petiole terete, canaliculate adaxially, 2.0–4.8 cm long, glandular dotted with tiny resinous glands and with scattered villous trichomes adaxially, especially on the ridges of the petiole; terminal leaflet elliptic, 7.5–13.8 cm long, 1.8–3.5 cm wide; lateral leaflets ovate to elliptic, asymmetrical near the base, long acuminate and emarginate at the apex, 3.5–11.5 cm long, 1.4–3.8 cm wide, glandular dotted above and beneath, chartaceous to membranous, the lateral veins 6 to 9 pairs, moderately ascending and weakly anastomosing, conspicuous, glabrate. *Inflorescences* terminal and axillary; corymbs loose, few-flowered, peduncles erect to suberect, glabrous, 1.5–2.2 cm long. *Flowers* (not seen in Panamanian material) white; calyx campanulate, glandular punctate, 3.2–4.0 mm long, the lobes ovate, the apex acute, 2.5–3.0 mm long, corolla 1.3–1.6 cm long, the tube slightly flaring, slender, straight in bud, 9–11 mm long, the lobes imbricate, oblong to narrowly obovate, the apex obtuse, spreading, 4–5 mm long; stamens 5–7, included, inserted about midway on the corolla tube, the filaments 3–4 mm long, fertile anthers 2, 5–6 mm long, basifixed, longitudinally dehiscent; staminodes 5, free, linear; ovary 5-carpellate, the style cylindrical, 1.8–2.0 cm long, the stigma 5-lobed but often appearing as 1, 1.0–1.5 mm long. *Capsules* of 5 carpels united only at the base, each carpel oblong to subtriangular; endocarp cartilagenous, bivalvate, 1-seeded; seeds oblong, slightly compressed.

This species occurs in Guyana, French Guiana, Colombia, and it extends into Panama only in Darien.

DARIÉN: La Palma, *Pittier 5710* (F, US).

6. HORTIA

Hortia Vandelli, Fl. Lus. et Bras. 14. 1788; Roem. Script. 188. 1796. TYPE: *Hortia brasiliensis* Vandelli ex A. P. DC.

Shrubs or medium sized *trees*, usually up to 20 m high. *Leaves* alternate, simple, often 10–24 cm long, oblanceolate to obovate, entire; veins often prominent on the lower surface, coriaceous to rigid, glabrous to pilose. *Inflorescences* terminal, broadly paniculate to corymbose, drying reddish brown and with a conspicuous reticulate epidermis, generally many flowered. *Flowers* small, red, rose, or violet, bisexual, 5-merous, regular, pedicellate; calyx cupular, shortly 5-lobed, coriaceous; corolla lobes free, oblong, coriaceous, the apices inflexed, valvate in bud; stamens 5, free, all fertile, inserted at the base of the 5-lobed nectary, the filaments free, filiform, the anthers oblong, dorsifixed; ovary often ellipsoid, 5-locular, each locule with 2 superposed ovules. *Fruits* drupaceous, usually oval, 5-locular; seeds generally 2 per locule, oblong, black.

This small genus of perhaps eight species is largely Brazilian, with a single species from Panama and Colombia.

1. **Hortia colombiana** Gleason, Phytologia 1: 25. 1933. TYPE: Colombia, *Lawrance* 392 (NY).

Trees 8–30 m high, the trunk 6–20 cm in diam.; young branchlets terete, thick, stout, brown to reddish brown, marked with conspicuous leaf scars, glabrous. *Leaves* clustered toward the apex of the branchlets, obovate to oblong obovate, 16–28 cm long, 4.0–6.8 cm broad, subacute to rounded at the apex, long cuneate at the base, covered with numerous but inconspicuous glandular punctations on the lower surface, narrowly revolute, chartaceous to almost coriaceous, glabrous, pinnately veined with 20–28 primary pairs, moderately ascending, anastomosing and conspicuous beneath; petioles 1.5–2.5 cm long, semi-terete, canaliculate adaxially, narrowly winged, stout, usually swollen at the base. *Inflorescences* terminal?, broadly corymbiform, many branched and many flowered, the peduncles short, stout, erect, glabrous, 2–3 cm long, sulcate, reddish brown when dry, the epidermis conspicuously reticulate. *Flowers* rose to rose red, the pedicels stout, rugose, 1.5–2.0 mm long; calyx shallowly campanulate, coriaceous to fleshy, faintly pellucid punctate, the lobes broadly rounded and with a slight irregular margin; corolla of 5 free lobes, rose pink to rose red, thick, ovate oblong, 5–6 mm long, 2.2–2.6 mm wide, with a terminal 1 mm linear inflexed apicule, each lobe with a densely bearded pulvinus below the middle; stamens 5, inserted in the lobes of the nectary, the filaments stout, 2.5–3.0 mm long, the anthers oblong, 1.8–2.2 mm long; ovary ovoid, 5-locular, the style short, the stigma simple, the ovary surrounded at the base by a 5-lobed nectary. *Fruits* not seen.

COLÓN: Santa Rita Ridge road 4 mi from Transisthmian Highway to Agua Clara weather station, *Gentry et al.* 8848 (MO).

7. MURRAYA

Murraya Koenig ex L., Mant. 2: 554. 1771. "Murraea" nomen et orthogr. cons. vs. *Camunium* Adanson, *Chalcas* L., and *Bergera* L. TYPE: *M. exotica* L.

Camunium Adanson, Fam. 2: 166. 1763. nomen rejic. TYPE: *C. paniculata* L. nomen rejic.
Chalcas L., Syst. Nat., ed. 12. 293. 1767. nomen rejic. TYPE: *C. paniculata* L.
Bergera Koenig ex L., Mant. 2: 555. 1771. nomen rejic.

Unarmed *shrubs* or small *trees*. *Leaves* alternate, odd-pinnate; leaflets alternate or subopposite. *Inflorescences* axillary or terminal panicles or cymes, or the flowers solitary. *Flowers* (4–)5-merous; sepals (4–)5, ovate or lanceolate, connate basally; petals (4–)5, lanceolate to spatulate or linear, imbricate or valvate; stamens (8–)10, elongate, the filaments sometimes flattened, free, inserted on the disc, the anthers small, broadly elliptic or oval; disc annular, cushion shaped or cylindrical; ovary syncarpous, ovoid, 2–5-loculed, the ovules (1–)2 per locule, superposed or almost collateral, the style elongate, slender, finally deciduous, the stigma capitate. *Fruit* a small ovoid or subglobose berry, the pulp mucilaginous; seeds 1–several, the testa thin, the cotyledons plano-convex.

Murraya is a genus of 11 species occurring in southeastern Asia and Oceania from India and southern China to northeastern Australia and New Caledonia. Several species are cultivated as ornamentals in the tropics.

FIGURE 6. *Murraya paniculata* (L.) Jack—A. Habit (×1⅓).—B. Fruit (×2⅗). [A after *Tyson 1301* (MO). B after *Tyson 3466* (MO).]

Literature:

Swingle, W. T. & P. C. Reece. 1967. *Murraya*. Pp. 231–252 *in* W. Reuther et al. (Editors), The Citrus Industry. Vol. 1. History, World Distribution, Botany, and Varieties. rev. ed. Berkeley.

Jackson, B. 1912. Index to the Linnean Herbarium. Linn. Soc. London Proc. 124th session, Suppl. 152 pp.

1. **Murraya paniculata** (L.) Jack, Malay. Misc. 1: 31. 1820.—LECTOTYPE: British India, (LINN 539.1 or 539.2 not seen). cf. Jackson, 1912, p. 100; Swingle & Reece, 1967, p. 233.—FIG. 6.

Chalcas paniculata L., Mant. 1: 68. 1767.
Murraya exotica L., Mant. 2: 563. 1771.
Camunium exoticum (L.) Kuntze, Rev. Gen. Pl. 1: 99. 1891.
Chalcas exotica (L.) Millsp., Publ. Field Columbian Mus., Bot. Ser. 1: 25. 1895.

Aromatic *shrubs* or *trees*, 3–10 m high, the foliage dense, the branchlets glandular punctate, puberulent to glabrate. *Leaves* odd pinnate, 4–11 cm long; petioles and rachises puberulent; leaflets alternate or rarely subopposite, obovate, obtuse or rounded to abruptly blunt acuminate and usually retuse apically, cuneate basally, the margins entire, revolute, dark green above, paler beneath, coriaceous, puberulent to glabrate, glandular punctate, the punctations numerous over the entire blade, 11–43 mm long, 7–24 mm wide; petiolules puberulent, to 2 mm long. *Inflorescences* dense, puberulent, 2.5–4.5 cm long. *Flowers* 5-merous, fragrant, the pedicels to 3 mm long; sepals 5, triangular, puberulent, ca. 1 mm long, connate for about ½ their length; petals 5, white, oblanceolate to spatulate, recurved, glandular punctate, pubescent or glabrous, tomentulose apically, 12–19 mm long, 5–6 mm wide; stamens 10, alternately shorter, the filaments subulate, 6 and 9 mm long; disc prominent, fleshy; ovary glandular punctate, glabrous, ca. 2 mm high, the style deciduous, the stigma capitate, 1 mm in diam. *Fruit* a red drupaceous berry, ovoid, acuminate apically, glandular punctate, verrucose, glabrous, 1 cm long; seed 1.

The orange jessamine is native to southeastern Asia. *Murraya paniculata* is cultivated throughout the tropics for its large white fragrant flowers and showy red berries. It is often used as a hedge plant, and has become naturalized in many areas. In Panama it is known as *mirto* (fide *Standley 30531*).

The collections cited all presumably were escapes from cultivation, although only *Standley 25314* was noted as "wild." The collections bearing an asterisk apparently represent cultivated material.

BOCAS DEL TORO: Little Bocas, *Wedel 2542* (GH, MO, US). CANAL ZONE: Behind BMI office, Balboa Heights, *Duke 10758** (MO). Planted, Balboa, *Standley 30840** (US). Ornamental, Survival School area, *Tyson 1301** (MO). Curundu, at house 2114, *Tyson 3466** (MO). PANAMÁ: Isla Chepillo, *Duke 10332* (MO). Coastal thicket, Bella Vista, *Standley 25314* (US). Planted, Juan Diaz, *Standley 30531** (US). Isla Taboga, *Woodson et al. 1516* (A, F, MO, US).

8. TICOREA

Ticorea Aubl., Hist. Pl. Gui. Franc. 2: 689, *tab. 277*. 1775. TYPE: *T. foetida* Aubl.

Trees or *shrubs*, usually less than 10 m high. *Leaves* alternate to subopposite, (1–)3(–4)-foliolate, the terminal leaflet larger than the laterals, often oblong elliptic, attenuate at the base, acuminate at the apex, the lateral leaflets smaller, oblique at the base, acuminate at the apex. *Inflorescences* terminal to upper axillary, corymbose to corymbose paniculate, few to many flowered, usually long pedunculate. *Flowers* large, white to cream, bisexual, 5-merous, regular; calyx cupular with 5 equal lobes; corolla united into a long to short cylindrical tube, the petals usually oblong, obtuse to acute at the tip, imbricate in bud, erect to slightly spreading at maturity; stamens 5, all fertile, the anthers oblong, erect, longitudinally dehiscent, basifixed, the filaments adnate to the base of the petals;

ovary obovate, 5-carpellate, free, the ovules 2 per locule, superimposed, the ovary surrounded by a cupular nectary, the style filiform, the stigma subclavate. *Fruits* of 1–5 free mericarps, each mericarp oblong, dehiscing longitudinally; endocarp free, falling from the mericarp at maturity, winged; seeds 1 per mericarp; oblong.

Ticorea is a South American genus containing but a few species with one species, *Ticorea unifoliolata*, reaching Panama. This genus is closely related to both *Angostura* and *Galipea*.

1. **Ticorea unifoliolata** Elias.[7] TYPE: Panama, *Dressler 3860* (MO, holotype; NY, isotype).—FIG. 7.

Small *trees* 5–10 m high; branches terete, reddish brown but becoming gray with age, conspicuously lenticellate. *Leaves* unifoliolate, elliptic, 14–24 cm long, 6–12 cm broad, acuminate at the apex, attenuate at the base with numerous, tiny, glandular punctations, subcoriaceous to coriaceous, glabrous, pinnately veined, the veins 7–10 pairs, moderately ascending, anastomosing, conspicuous beneath; petioles 1.5–9.5 cm long, terete, stout, articulated just below the base of the lamina, slightly swollen and drying dark brown to reddish brown at the point of articulation. *Inflorescence* corymbiform, rounded, usually terminal, 16–24 flowered; peduncles erect, (3–)5–10 cm long, elongating to 15–25 cm long in fruit, stout, glandular dotted, glabrous. *Flowers* cream, bisexual, 5-merous, regular, pedicellate, the pedicel 5–7 mm long, tapering into the calyx tube, the calyx campanulate to cup shaped, 3–5 mm long, glabrous, the lobes scarcely discernable, persistent in fruit; corolla lobes free, oblong, 9–12 mm long, ca. 3 mm broad, rounded at the apex, slightly cucullate, dotted on the upper ½; stamens 5, all fertile, the anthers narrowly oblong, pointed at the apex, 5–6 mm long, basifixed, pilose at the base of the anther, the filaments flattened, 4–5 mm long, inserted at the base of the disc; style 1, cylindrical, 5–6 mm long, terminated by a small 5-lobed stigma, the ovary consisting of 5 carpels, each carpel free except near the base, the carpels tightly enclosed in a cup shaped nectary. *Fruits* 1–5 mericarps, oblong to reniform, rounded at the apex, with conspicuous transverse ridges, glabrous, dehiscing longitudinally from the apex, 1.8–2.2 cm long, 1.2–1.5 cm wide, attached to the receptacle; endocarp free and dehiscing from the persistent mericarp at maturity, the endocarp with 2 oblong, round-tipped wings, each wing 8–12 mm long, stramineous, partially enclosing the seed at the base; seed oblong to reniform, 8–11 mm long, 5–6 mm broad, rounded, smooth, drying dark brown.

This species appears to be restricted to eastern Panama but is expected to occur in Darien, the San Blas, and neighboring areas in Colombia.

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[7] *Ticorea unifoliolata* Elias, sp. nov. *Arbor* 5–10 m alta. *Folia* alterna, unifoliolata, petiolis 1.5–9.5 cm longis, lamina elliptica, 14–24 cm longa, 6–12 cm lata, acuminata, cuneata, utrinque glandulosa. *Inflorescentiae* terminales, corymbosae, 16–24 floridae, pedunculis 5–10 cm longis. *Flores* 5-merous, calyce campanulato, 3–5 mm longo, glabro, corollae lobis libris, 9–12 mm longis, staminibus 5, liberis, inclusis, ovario 5-carpellato. *Mericarpia* 5, libra, reniformia, endocarpio bivalvato; seminibus 8–11 mm longis.

FIGURE 7. *Ticorea unifoliolata* Elias—A. Flowering branch (×½)—B. Flower and bud (×1)—C. Fruiting branch with unifoliolate leaves (×½)—D. Dehiscent capsule (×½)—E. Endocarp with seed (×⅔)—F. Seed (×⅔). [A, B after *Dressler* 3888 (MO); C, D, E, F after *Dressler 3860* (MO).]

COLÓN: Between Aqua Clara rain gauge and Puerto Pilón, *Dressler* 3935 (MO). Santa Rita lumber road, upper Río Mango Indio, M of Aqua Clara, *Dressler 3860* (MO, NY). Near Aqua Clara rainfall station, Santa Rita Ridge, *Foster 1731* (MO). PANAMÁ: Cerro Jefe, headwaters of Río Cascadas, *Correa & Dressler 1645* (MO, NY); *Dressler* 3888 (MO, NY). Cerro Jefe near Río Indio, *Duke 15225* (MO).

9. ZANTHOXYLUM

Zanthoxylum L., Sp. Pl. 270. 1753; Gen. Pl., ed. 5, 130. 1754.[8] TYPE: *Z. americanum* Mill.

Fagara Duhamel, Traité Arb. Arbust. 1: 229. 1755. nomen rejic. contra *Fagara* L. New name for *Zanthoxylum* L.
Pterota P. Br., Nat. Hist. Jamaica 146. 1756. TYPE: *Fagara pterota* L.
Fagara L., Syst. Nat., ed. 10, 2: 897. 1759. nomen cons. contra *Fagara* Duhamel. TYPE: *F. pterota* L., type cons.

Shrubs or *trees*, rarely scandent; trunks and branches often armed with prickles, the branchlets prickly or unarmed, the bark and wood aromatic. *Leaves* alternate, odd- or even-pinnate, rarely 1–3 foliolate, persistent or deciduous; petiole and rachis terete or angled, often winged, unarmed or prickly; leaflets opposite to alternate, entire to crenate, frequently inequilateral, pellucid punctate at least marginally, often glandular punctate and with numerous minute peltate scales on both surfaces. *Inflorescences* axillary and/or terminal panicles, sometimes corymbose, racemose, or spikelike. *Flowers* small, regular, white to greenish yellow or red, unisexual or rarely bisexual, the plants dioecious, rarely monoecious or polygamous; sepals 3–5 or apparently absent, free to connate, persistent or deciduous; petals 3–8, free, imbricate or valvate; stamens 3–5, opposite the sepals, rudimentary or absent in carpellate flowers, the filaments free, unappendaged, the anthers elliptic to ovate; intrastaminal disc small and annular or obscure; gynoecium of 1–5, sessile to stipitate, free or connate carpels, rudimentary or absent in staminate flowers; ovary 1–5-loculed, the ovules 2 per locule, collateral, pendulous, the styles sublateral, connate to free, the stigmas capitate, free or connate. *Fruits* of 1–5 sessile to stipitate, coriaceous to fleshy, 2-valved, 1-seeded, free to connate, glandular-punctate follicles; seeds ovoid, obovoid, subglobose, or lenticular, often remaining attached to the placenta by the funiculus at maturity, the testa crustaceous, black, brownish, or reddish, lustrous, the endosperm fleshy, the embryo axial, straight or curved, the cotyledons flat, the radicle short.

Zanthoxylum is a genus of over 200 species, primarily pantropical, but extending into the North Temperate Zone in eastern Asia and North America.

The genus as here circumscribed is regarded by some as two distinct genera, *Zanthoxylum* L. and *Fagara* L. The name *Zanthoxylum* is applied to species with a single whorl of perianth segments, while *Fagara* is used for those with two whorls of perianth segments. However, the occurrence of specimens and species of an intermediate condition (Brizicky, 1962; Hartley, 1966) and recent chemical evidence (Fish and Waterman, 1973) indicate that this is an unnatural separation. The American species of *Zanthoxylum* are badly in need of revision.

Literature:

Brizicky, G. K. 1962. Taxonomic and nomenclatural notes on *Zanthoxylum* and *Glycosmis* (Rutaceae). J. Arnold Arbor. 43: 80–93.

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[8] Further generic synonymy will be found in Wilson, N. Amer. Fl. 25: 177. 1911.

Fawcett, W. & A. B. Rendle. 1920. Rutaceae *in* Flora of Jamaica, Vol. 4. pp. 168–195.

Fish, F. & P. G. Waterman. 1973. Chemosystematics in the Rutaceae II. The chemosystematics of the *Zanthoxylum/Fagara* complex. Taxon 22: 177–203.

Hartley, T. G. 1966. A revision of the Malasian species of *Zanthoxylum* (Rutaceae). J. Arnold Arbor. 47: 171–221.

Wiggins, I. L. & D. M. Porter. 1971. Flora of the Galapagos Islands. Stanford, California.

a. Leaf petioles and rachises winged ..... 5. *Z. fagara*
aa. Leaf petioles and rachises not winged.
  b. Leaves pubescent with stellate trichomes.
    c. Leaflets oblong to oblong lanceolate, the margins crenulate ..... 1. *Z. belizense*
    cc. Leaflets narrowly elliptic, the margins coarsely crenate ..... 9. *Z. microcarpum*
  bb. Leaves glabrous or pubescent with simple trichomes.
    d. Leaflets pellucid punctate throughout the blade.
      e. Leaflets glabrous.
        f. Leaflets 3; flowers 4-merous ..... 7. *Z. limoncello*
        ff. Leaflets 9–13; flowers 5-merous ..... 3. *Z. elephantiasis*
      ee. Leaflets pubescent, at least on the main veins beneath.
        g. Leaflets hispidulous beneath, especially on the veins; flowers 5-carpelled ..... 15. *Z. setulosum*
        gg. Leaflets minutely puberulent or strigillose to scabridulous beneath; flowers 3–4-carpelled.
          h. Leaflets scabridulous; inflorescence branches red tomentose ..... 11. *Z. pittieri*
          hh. Leaflets minutely puberulent to strigillose; inflorescence branches minutely puberulent to strigillose, the trichomes yellow or white.
            i. Leaflets 2.5–6.5 cm long, 1.3–2.7 cm wide; carpels free, the mature follicles 1 per flower ..... 6. *Z. jaimei*
            ii. Leaflets 5.5–22.0 cm long, 2.9–8.5 cm wide; carpels connate, the mature follicles mostly 3 per flower.
              j. Leaflets 9–14; follicles strigillose ..... 10. *Z. panamense*
              jj. Leaflets 7; follicles glabrous ..... 4. *Z. eliasii*
    dd. Leaflets pellucid punctate only at the margins.
      k. Leaflets minutely puberulent above along the impressed midveins.
        l. Leaflets markedly inequilateral basally; flowers red, sepals with a conspicuous red abaxial gland; follicles glabrous ..... 2. *Z. chiriquinum*
        ll. Leaflets not markedly inequilateral basally; flowers greenish yellow to white, sepals without an abaxial gland; follicles minutely puberulent.
          m. Leaflets (3–)7–9(–10), subcoriaceous, with many small impressed punctations on both the surfaces ..... 14. *Z. scheryi*
          mm. Leaflets 5–7, thick and coriaceous, with many small impressed punctations and peltate glands on both the surfaces ..... 8. *Z. melanostictum*
      kk. Leaflets glabrous.
        n. Leaflets membranaceous, the margins crenate; flowers 5-merous ..... 13. *Z. pucro*
        nn. Leaflets subcoriaceous to coriaceous, the margins crenulate; flowers 3-merous.
          o. Leaflets 7.5–21.0 cm long, 2.3–7.2 cm wide ..... 12. *Z. procerum*
          oo. Leaflets 2.2–7.2 cm long, 0.8–1.8 cm wide ..... 16. *Z. tripetalum*

1. **Zanthoxylum belizense** Lundell, Contr. Univ. Michigan Herb. 6: 35. 1941. TYPE: Belize, *Gentle 3431* (MICH).

Trees, 3.5–35.0 m high; trunks armed with horizontally flattened prickles, the branchlets stellate pubescent. *Leaves* odd- or even-pinnate, 30–150 cm long; petiole and rachis sometimes armed with small prickles, stout, squarish, reddish to whitish stellate pubescent, becoming almost glabrate; leaflets 17–26, subopposite to alternate, oblong to oblong lanceolate, abruptly acuminate apically, obliquely rounded basally, the margins obscurely crenulate and revolute, the blade pellucid punctate throughout, chartaceous, shiny and becoming sparingly whitish stellate pubescent above, duller and densely whitish stellate pubescent beneath, the pubescence on the midvein reddish to whitish, 53–210 mm long, 18–72 mm wide, subsessile to obscurely petiolulate. *Staminate panicles* axillary, widely branched, 26 cm long, the branches brown, thick, whitish to reddish stellate pubescent. *Staminate flowers* yellowish green, aromatic, the pedicels 1 mm long; sepals 5, triangular, ciliate, less than 1 mm long; petals 5, elliptic, acute, imbricate, 1.5 mm long, less than 1 mm wide; stamens 5, exserted, 4 mm long; ovary 5-lobed, pyramidal, pubescent, 1 mm high, the style short, the stigma lobed. *Carpellate panicles* axillary, branched, 21 cm long, the branches brown, thick, stellate pubescent. *Carpellate flowers* with the pedicels ca. 1.5 mm long in fruit; sepals 5, triangular, stellate pubescent, ciliate, less than 1 mm long; stamens 5, sterile; carpels 2, free, pubescent, the style less than 1 mm long, the stigma capitate. *Follicles* 1, globose, punctate verrucose with many minute punctate scales, ca. 4 mm in diameter.

Zanthoxylum belizense occurs from the Mexican states of Vera Cruz and Oaxaca through Belize, Guatemala, Honduras, Nicaragua, and Costa Rica to Panama, and perhaps into Colombia. In Panama it is known to flower in August through October, and to fruit in January and March.

Croat 16719 has leaves which are sparsely stellate pubescent on their abaxial surfaces and more markedly crenulate than usual. Perhaps it represents a hybrid individual.

This is a species of monsoon forest and evergreen seasonal forest, occurring on the Caribbean side of the Isthmus. It has often been confused with *Zanthoxylum microcarpum*, but the two are distinguished by the differences enumerated in the key to species above. *Zanthoxylum belizense* is known as *arcabu* (fide *Howell 33* and *Standley 27603*); *obo de monte* (fide *Gomez-Pompa et al. 2949*); and *tachuelo* (fide *Howell 33*).

CANAL ZONE: Pipeline Road, *Lao et al. 28* (MO). Hills N of Frijoles, *Standley 27603* (US). 10 mi E of Gamboa bridge, *Stern & Chambers 17* (MO, US). 7 mi N of Gamboa, *Tyson 6636* (MO). 10 mi N of Gamboa, *Tyson 6654* (MO). BARRO COLORADO ISLAND: *Croat 8071* (MO), *9146* (MO, SCZ), *9788*, *10936* (both MO), *12497* (DUKE, MO, SCZ); *Foster 1466* (DUKE, MO); *Kenoyer 401* (US). COLÓN: Santa Rita, cuadro de muestro No. 1, 200–300 m, *Gomez-Pompa et al. 2949* (MO). SAN BLAS: Hills SE of Puerto Obaldía, *Croat 16719* (MO).

2. **Zanthoxylum chiriquinum** Standley, Field Mus. Nat. Hist., Bot. Ser. 18: 569. 1937. TYPE: Panama, *Pittier 3060* (F, holotype; F, US, isotypes).

Shrubs or small *trees* 1.5–2.5 m high; branchlets brownish, occasionally with small brown prickles to 3 mm long, younger parts covered with minute red

glandular trichomes, becoming glabrate. *Leaves* odd pinnate, 9–30(–42) cm long; petiole 20–94 mm long, the petiole and the rachis canaliculate above, minutely puberulent to glabrous in the sulcus; leaflets (3–)5–13(–17), opposite, elliptic to narrowly obovate, acute to obtuse and retuse to occasionally emarginate apically, acute, decurrent and usually markedly inequilateral basally, the margins crenate, the blade conspicuously pellucid punctate marginally at the bases of the crenations and with many small impressed punctations on both the surfaces, subcoriaceous, usually minutely puberulent above along the impressed midrib, the midrib conspicuous beneath, 24–120 mm long, 12–46 mm wide, the petiolules 2–35 mm long, those of the terminal leaflets longest. *Staminate panicles* reddish, axillary, solitary, with minute red glandular trichomes, 8–15 cm long. *Staminate flowers* red, the pedicels 2–4 mm long; sepals 5, broadly triangular, acute, spreading, the margins hyaline and revolute, ca. 1 mm long with a conspicuous dark red abaxial gland; petals 5, oblong, 4 mm long, 2 mm wide, the margins hyaline with a subapical abaxial gland; stamens 5, 3 mm long; carpels 5, rudimentary, less than 1 mm long. *Carpellate panicles* reddish, axillary, corymbose, 3–16 cm long in fruit. *Carpellate flowers* red (sometimes greenish white?), the pedicels 5–6 mm long; sepals 5, obtuse triangular, ca. 1 mm long, the margins hyaline with a conspicuous dark red abaxial gland; carpels 5, free, puberulent, stipitate, the style less than 1 mm long, the stigma capitate. *Follicles* (1–)3–5, subglobose, red becoming brown, roughened, punctate glandular, 7–8 mm long, the stipe 2–5 mm long; seeds black, lustrous.

This species occurs in Panama and Costa Rica. In Panama it is known to flower in May and to fruit in March, July, and August.

This species, *Zanthoxylum scheryi*, and *Z. melanostictum*, occur in the cloud forests of Chiriqui Province. They are similar morphologically and may be easily confused with one another. However, they appear to be distinct ecologically and spatially. *Zanthoxylum chiriquinum* and *Z. melanostictum* occur at lower elevations than does *Z. scheryi*; *Z. chiriquinum* appears to grow under less moist conditions, and hence the three species are allopatric.

CHIRIQUÍ: Above San Félix along mining road 18–27 mi off Panamerican Highway, 1200–1500 m, *Croat 33103* (MO). Cerro Colorado copper mine development, 28 mi above San Félix, 9–10 mi above turnoff to Escopeta, 1200–1500 m, *Croat 33250* (MO). Monte Rey, *Croat & Porter 15878* (MO). Cerro Hornitos, 40 km NW of Gualaca, 2238 m, *Mori & Bolton 7472, 7478* (both MO). Cerro Colorado, 50 km N of San Félix on continental divide, 1200–1500 m, *Mori & Dressler 7888* (MO). N of San Félix at Chiriquí-Bocas del Toro border on Cerro Colorado copper mine road, 5000–5500 ft, *Mori & Kallunki 5788* (MO). Río Ladrillo, 1200–1300 m, *Pittier 3060* (F, US).

3. **Zanthoxylum elephantiasis** Macfad., Fl. Jamaica 1: 193. 1837. TYPE: Jamaica, *Macfadyen* (K, not seen).

Fagara elephantiasis (Macfad.) Krug & Urb. in Urb., Bot. Jahrb. Syst. 21: 564. 1896.

Trees, 3–15 m high; trunks usually armed, the branchlets glabrous, unarmed. *Leaves* odd-pinnate, glabrous, to 26 cm long; petiole and rachis rounded, canaliculate above, glabrous; leaflets 9–13, opposite or subopposite, elliptic to narrowly ovate, acute to narrowly acuminate apically, obliquely rounded or acute and inequilateral basally, the margins crenulate, the blade pellucid punctate through-

out, the marginal punctations at the bases of the crenulations conspicuous, subcoriaceous, darker above, 59–85 mm long and 22–40 mm wide, the petiolules canaliculate above, 2–8 mm long. *Panicles* terminal and axillary, compact, 1.5–5.5 cm long, the peduncles and branches glabrous, thick, drying to form reddish brown and whitish horizontal stripes. *Staminate flowers* with the pedicels to 1 mm long; sepals 5, suborbicular, obtuse, marginally scarious and irregular, ca. 1 mm long, to 2 mm wide; petals 5, elliptic oblong, obtuse, imbricate, 5–6 mm long; stamens 5, about as long as the petals; disc 5-lobed; ovary 5-lobed, rudimentary. *Carpellate flowers* like the staminate, except the stamens absent; carpels 5, connate. *Follicles* (1–)5, obovoid, punctate verrucose, glabrous, stipitate, 6–8 mm in diameter, the stipe 3–8 mm long; seeds black, lustrous.

The single specimen known from Panama is staminate. Details of carpellate flowers and fruits given above are from Fawcett and Rendle (1920) in part.

Zanthoxylum elephantiasis is known from the Greater Antilles, Costa Rica and Panama. In Panama it is known to flower in January or February. This species was collected in an area of thorn forest, the driest in Darien.

When describing *Zanthoxylum elephantiasis*, Macfadyen stated, "I have given the specific name, from the resemblance of the bark of the stalk of the panicle, to the appearance of the skin of the feet in elephantiasis." This characteristic of the panicles renders the species easily recognizable when in flower or fruit.

DARIÉN: Near sea level, Garachiné, *Pittier 5693* (GH, US).

4. **Zanthoxylum eliasii** D. M. Porter, J. Arnold Arbor. 53: 403. 1972. TYPE: Panama, *Duke & Elias 13851* (MO, holotype; F, GH, isotypes).

Spindly *trees*; branchlets glabrous. *Leaves* odd-pinnate; petiole and rachis together 15–32 cm long, canaliculate above, minutely puberulent to glabrate; leaflets 7, opposite to subopposite, ovate to oval, abruptly acuminate apically, inequilateral and more or less rounded basally, the margins entire, the blade pellucid punctate throughout, subcoriaceous, minutely and sparingly puberulent below on the veins, 10–22 cm long, 5.5–8.5 cm wide, the petiolules canaliculate above, to 1 cm long. *Staminate flowers* unknown. *Carpellate panicles* stout, axillary, minutely puberulent, 7.5–16.5 cm long, to 10 cm wide in fruit. *Carpellate flowers* with the pedicels stout, minutely puberulent, 4–7 mm long in fruit; sepals 5, triangular, less than 1 mm long; carpels 3(–4), connate. *Follicles* (1–)3(–4), subglobose, sessile, more or less beaked, connate basally, punctate glandular, glabrous, ca. 5 mm in diameter, red at maturity; seeds subglobose, black, lustrous, ca. 5 mm in diameter.

This species is known only from the type collection, fruiting in August.

DARIÉN: Cerro Pirre, cloud forest and/or mossy forest, 2500–4500 ft, *Duke & Elias 13851* (F, GH, MO).

5. **Zanthoxylum fagara** (L.) Sarg., Gard. & Forest 3: 186. 1890.

Schinus fagara L., Sp. Pl. 389. 1753. TYPE: Figure in Sloane, Voyage 2: *pl. 162*, f. 1. 1725.
Fagara pterota L., Syst. Nat., ed. 10, 2: 897. 1759. TYPE: Same as for *Schinus fagara* L.

Pterota fagara (L.) Crantz, Inst. Rei Herb. 2: 417. 1766.
Fagara lentiscifolia Humb. & Bonpl. ex Willd., Enum. Pl. 165. 1809. TYPE: B, not seen.
Zanthoxylum pterota (L.) H.B.K., Nov. Gen. Sp. Pl. 6: 3. 1823.
Z. lentiscifolium (Willd.) Anderss., Kongl. Svensk. Vet.-Akad. Handl. 1853: 244. 1855. not *Z. lentiscifolium* Champ. ex Benth., Hook. J. Bot. 3: 329. 1851.
Fagaras fagara (L.) Kuntze, Rev. Gen. Pl. 3(2): 34. 1898.
Fagara fagara (L.) Small, Fl. SE. U.S. 675. 1903.

Shrubs or small *trees* to 10 m high; branchlets zigzagged, reddish brown, becoming light gray, minutely puberulent to glabrate, more or less angled, sometimes ridged between the nodes, armed with paired, subulate, recurved, sharp, dark, minutely puberulent, deciduous, pseudostipular prickles 2–6 mm long. *Leaves* odd-pinnate, 4–9 cm long, 2–4 cm wide; petiole and rachis winged, canaliculate above, more or less minutely appressed puberulent to glabrate, the petiole 11–24 mm long, ca. 2 mm wide, the rachis 3–6 mm wide; leaflets 5–7, opposite to subopposite, obovate to broadly elliptic, acute to rounded and retuse apically, inequilateral and cuneate basally, the margins crenulate and revolute, the blade pellucid punctate marginally at the bases of the crenulations, membranaceous to subcoriaceous, sparingly minutely appressed puberulent to glabrate, 9–35 mm long, 6–21 mm wide, the lowest pair smallest, sessile to short petiolulate, the terminal leaflet decurrent to the rachis. *Panicles* axillary, spikelike, minutely puberulent, to 2 cm long. *Staminate flowers* subsessile; sepals 4, broadly obovate, ca. 1 mm long; petals 4, obovate; stamens 4, less than 1 mm long. *Carpellate flowers* with the pedicels to 1 mm long in fruit; sepals 4, broadly obovate, ca. 1 mm long; petals 4, obovate; carpels 2, sessile, connate basally, ca. 1 mm long. *Follicles* 1, obovoid, brownish, roughened, with brownish punctations, glabrous, ca. 5 mm in diameter, short stipitate, the stipe 2 mm long.

The single collection known from Panama is in fruit. Details of the flowers given above are from Wiggins and Porter (1971).

Zanthoxylum fagara is a widespread species, occurring from Florida and Texas southward through Mexico and the Caribbean region to Peru and northern Argentina. In Panama, this species is known to fruit in December.

Detailed study of the species throughout its range may support the recognition of several taxa.

PANAMÁ: La Jagua, *McDaniel 8211* (DUKE).

6. **Zanthoxylum jaimei** D. M. Porter, J. Arnold Arbor. 53: 406. 1972. TYPE: Panama, *Duke & Elias 13793* (MO).

Trees; trunks apparently armed, the branchlets armed with small brownish prickles, minutely puberulent. *Leaves* apparently odd-pinnate; petiole and rachis together 3–10 cm long, minutely puberulent especially toward the base; leaflets 9–11, opposite(?), elliptic to obovate, abruptly acuminate apically, inequilateral and cuneate basally, the margins crenulate, the blade pellucid punctate throughout, coriaceous, minutely puberulent, especially along the impressed midvein above and on the blade beneath, 25–65 mm long, 13–27 mm wide, the petiolules ca. 1 mm long. *Staminate flowers* unknown. *Carpellate panicles* axillary, 15 cm

long in fruit, the main branch armed with small brownish prickles, minutely puberulent. *Carpellate flowers* with the pedicels minutely puberulent, 1–2 mm long in fruit; sepals 5, triangular, apiculate, minutely puberulent, less than 1 mm long; carpels 3, free. *Follicles* 1, subglobose, shortly stipitate, punctate glandular, glabrous, 3–4 mm in diameter.

This species is known only from the type collection, fruiting in August.

DARIÉN: Cerro Pirre, cloud forest and/or mossy forest, 2500–4500 ft, *Duke & Elias 13793* (MO).

7. **Zanthoxylum limoncello** Tr. & Planch. ex Planch. & Oerst., Ann. Sci. Nat. Bot., Sér. 5, 14: 312. 1872. TYPE: Panama, Boquete, *Seemann 1655* (BM, not seen; photo NY).

Zanthoxylum costaricense Donnell Smith, Bot. Gaz. 13: 190. 1888. TYPE: Costa Rica, *Cooper 176* (F? not seen).
Fagara limoncello (Planch. & Oerst.) Engl., Nat. Pflanzenfam. 111. 4: 117. 1896.
Fagara costaricensis Engl., Bot. Jahrb. Syst. 21, Beibl. 54: 25. 1896. SYNTYPES: Costa Rica, *Hoffman 474, 475* (B?, neither seen).

Shrubs or small *trees*, 2–7 m high; trunks apparently armed, the branchlets glabrous, usually armed with brownish, recurved, 4–5 mm long, paired to occasionally solitary, pseudostipular prickles below the leaves. *Leaves* odd-pinnate, glabrous, 6–11 cm long; petiole and petiolules canaliculate above; leaflets 3, inserted at the top of the petiole, lanceolate to ovate or elliptic, acuminate apically, narrowed into the petiolule basally, the lateral leaflets inequilateral, the margins crenulate and slightly revolute, the blade pellucid punctate throughout, the marginal punctations at the bases of the crenulations conspicuous, coriaceous, paler beneath, 25–91 mm long, 11–32 mm wide, the terminal leaflets largest. *Staminate panicles* axillary, branched, minutely and sparsely puberulent, to 4.5 cm long. *Staminate flowers* green, subsessile or sessile; sepals 4, connate basally, broadly triangular, minutely puberulent, with a large subapical dorsal punctation, the margins hyaline, less than 1 mm long; petals 4, elliptic, with a large subapical dorsal punctation, the margins hyaline and ciliate, imbricate, ca. 2 mm long, 1 mm wide; stamens 4, exserted, 3–4 mm long; carpels 2, connate to the base of the style. *Carpellate panicles* axillary, branched, minutely and sparsely puberulent, 1.5–3.5 cm long. *Carpellate flowers* like the staminate, except the stamens absent; disc large, conspicuous, 3-lobed; carpels 3, free, obovoid, glabrous, the style ca. 1 mm long, the stigma capitate. *Follicles* 1–2, globose, punctate verrucose, glabrous, reddish at maturity, short stipitate, 4–5 mm in diameter; seeds black, lustrous, minutely pitted.

Zanthoxylum limoncello appears to occur only in Costa Rica and Panama; specimens from north of Costa Rica that have been attributed to this species represent another taxon. In Panama, this species is known to flower in March and to fruit in March and May. This is a plant of cloud forests.

CHIRIQUÍ: Old finca above upper end of Boquete, *D'Arcy 6470* (MO). Boquete, *Davidson 631* (A, F, US). Boquete, 1000–1300 m, *Maxon 5138* (NY, US). Pastures around Boquete, 1000–1300 m, *Pittier 3015* (NY, US). Valley of the upper Río Chiriquí Viejo, *White 27* (MO).

8. **Zanthoxylum melanostictum** Schlecht. & Cham., Linnaea 5: 231. 1830. TYPE: (?HAL, not seen).

Trees, 7–8 m high; trunks armed with large, scattered, conical prickles, the branchlets dark, glabrous, unarmed. *Leaves* odd-pinnate, 15–19 cm long; petiole 4–5 cm long, the petiole and the rachis canaliculate above, minutely puberulent in the sulcus; leaflets 5–7, opposite, elliptic to narrowly obovate, obtusely short acuminate, rounded and retuse or occasionally emarginate apically, acute and decurrent basally, the margins crenulate and revolute, the blade pellucid punctate marginally and with many small impressed punctations and peltate glands on both the surfaces, thick and coriaceous, minutely puberulent above along the impressed midrib, the midrib conspicuous beneath, 4–8 cm long, 15–29 mm wide, the petiolules canaliculate, 5–11 mm long, those of the terminal leaflets longest. *Staminate panicles* axillary and subterminal, solitary, minutely puberulent, to 6.5 cm long. *Staminate flowers* white, the pedicels minutely puberulent, ca. 1 mm long; sepals 5, triangular, spreading, the margins hyaline, less than 1 mm long; petals 5, oblong, the margins hyaline, 2 mm long; stamens 5; carpels 3, rudimentary, the styles connate, less than 1 mm long. *Carpellate panicles* axillary and subterminal, minutely puberulent, 6.0–7.5 cm long in fruit. *Carpellate flowers* not seen. *Follicles* 1–5, with minute orange glands, ca. 5 mm in diameter, the stipe ca. 2 mm long, minutely puberulent.

This species ranges from southern Mexico to Panama. In Panama it is known to flower in May.

VERAGUAS: Cerro Tuté, ca. 10 km NW of Santa Fé, 1000 m, *Mori 6282* (MO). 2 km from Escuela Agricola Alto de Piedra, below summit of Cerro Tuté, *Mori & Kallunki 5259* (MO).

9. **Zanthoxylum microcarpum** Griseb., Fl. Brit. W. Ind. 138. 1859. TYPE: Dominica, (?K, not seen).

Fagara microcarpa (Griseb.) Krug & Urb. in Urb., Bot. Jahrb. Syst. 21: 570. 1896.

Shrubs or *trees*, 2–20 m high; trunks armed, the branchlets stellate pubescent. *Leaves* odd-pinnate, 52 cm long, 20 cm wide; petiole canaliculate above, reddish, stellate pubescent and puberulent; leaflets 11–39, opposite to subopposite, narrowly elliptic, narrowly acuminate apically, cuneate and inequilateral basally, the margins coarsely crenate, the blade pellucid punctate throughout, firm membranaceous, stellate pubescent and puberulent, paler beneath, the midvein reddish, to 11.5 cm long, 2 cm wide, the petiolules ca. 1 mm long on the lateral leaflets and ca. 1 cm long on the terminal leaflets. *Panicles* terminal, much branched, mostly 10–15 cm long, the branches reddish, stellate pubescent. *Flowers* whitish; sepals 5, triangular, less than 1 mm long; petals 5, imbricate, 1.5–2.0 mm long; stamens 5, abortive in carpellate flowers; carpels 2 in carpellate flowers, the style less than 1 mm long, the stigma capitate. *Follicles* 1 or 2, subglobose, punctate verrucose, 4–5 mm in diameter; seeds compressed, black, lustrous.

The single collection known from Panama is sterile. Details of inflorescence, flowers, and fruits given above are, in part, after Standley and Steyermark (1946).

This species occurs from Chiapas, Mexico, along the Caribbean side of Central

America to northern South America, Trinidad, and the Lesser Antilles. *Zanthoxylum microcarpum* is perhaps not specifically distinct from *Z. rhoifolium* Lam. of Peru, Bolivia, Brazil, Paraguay, and Argentina.

PANAMÁ: Near Matías Hernández, *Standley 28961* (US).

10. **Zanthoxylum panamense** P. Wilson in Pittier, Contr. U.S. Natl. Herb. 20: 479. 1922.—Fig. 8. TYPE: Panama, *Pittier 3809* (US, holotype; GH, NY, US, isotypes).

Trees, 3–30 m high; trunks armed with more or less vertically flattened prickles, older trunks prickly only above, the branchlets strigillose to glabrate, sometimes armed with small sharp prickles. *Leaves* odd- or rarely even-pinnate, 17.5–38.5 cm long; petiole and rachis occasionally armed with yellowish prickles, canaliculate above, minutely puberulent to strigillose or glabrous; leaflets 9–14, opposite to subopposite, obovate or elliptic to oblong, abruptly acuminate or rounded apically, cuneate and inequilateral basally, the margins entire to obscurely crenulate, more or less revolute, the blade pellucid punctate throughout with punctations of 2 sizes, subcoriaceous, lustrous above and paler beneath, minutely puberulent or strigillose to glabrous, occasionally with 1 or more sharp yellowish prickles beneath on the midrib, 5.5–17.0 cm long, 2.9–8.0 cm wide, subsessile or the petiolule to 7 mm long. *Staminate panicles* axillary and crowded subterminally, many branched, to 25 cm long, the branches puberulent. *Staminate flowers* greenish white or white, the pedicels ca. 1 mm long; calyx 5-lobed, the lobes triangular, acute to rounded, puberulent, less than 1 mm long; petals 5, ovate or elliptic, acute, slightly keeled and thickened subapically, ca. 2.5 mm long, 1 mm wide; stamens 5, about as long as the petals; ovary 3-lobed, minutely pubescent, the styles 3, free, less than 1 mm long. *Carpellate panicles* terminal, branched, 8–14 cm long, the branches puberulent or strigillose. *Carpellate flowers* green, the pedicels ca. 1 mm long; calyx 5-lobed, the lobes triangular, acute, spreading, less than 1 mm long; petals 5, lanceolate, ca. 2 mm long, less than 1 mm wide; stamens abortive, less than 1 mm long; ovary 3-lobed, globose, the styles apical, connate, much less than 1 mm long, the stigma 3-lobed, discoid, 1 mm in diameter. *Follicles* 1–3(–4), subglobose, brown to dark red, punctate glandular, strigillose, 3–6 mm in diameter; seeds subglobose, black, lustrous, minutely pitted.

This species occurs in Panama and Costa Rica. In Panama it is known to flower in April, June, August, September, and October, and to fruit in April, May, July, August, September, November, and December.

Zanthoxylum panamense is a species of monsoon forest and evergreen seasonal forest found mainly on the Caribbean side of the Continental Divide. It may not be specifically distinct from *Z. kellermanii* P. Wilson of El Salvador, Guatemala, and British Honduras.

This species is known as prickly holly or yellow (*Cooper & Slater 41*) or acabu, alcabu, and arcabu, the latter also being applied to other members of the genus. Buttressing (*Croat 11834*), and ant-inhabited trunk prickles (*Croat 16539* and *Pittier 3809*), also are reported.

FIGURE 8. *Zanthoxylum*.—A.–B. *Z. panamense* P. Wilson.—A. Habit (×¾).—B. Fruits (×2¾). [A–B after *Shattuck H-1047* (US).]—C. *Z. procerum* Donn. Sm., fruit (×3½) [C after *Duke 14457* (MO).]

BOCAS DEL TORO: Almirante region, *Cooper & Slater 41* (F, US). Hill above railroad station at Milla 7.5, *Croat & Porter 16358, 16388* (both MO). CANAL ZONE: 4 mi from Gamboa gate, *Croat 15092* (MO). Boy Scout Road, Madden Dam, *Dwyer 6909* (MO). Without other locality, *Epplesheimer*, 1910 (F). Coco Solo, *Gentry 6290* (MO). Near Gatún railroad station, *Hayes 73* (NY). Mamei Hill, 20–90 m, *Pittier 3809* (GH, NY, US). Ft. Sherman, *Standley 31078* (US). Chagres River, 2–3 mi from mouth, *Stevens 1290* (US). Pipeline Road, N of Gamboa, *Tyson 6651* (MO). BARRO COLORADO ISLAND: *Carpenter 48* (F); *Croat 5466, 6249, 8907* (all MO), *11834* (DUKE, MO, SCZ), *11854, 12574, 14582, 14885, 16539* (all MO); *Foster 998, 1094* (both DUKE, MO); *Shattuck H-1047* (F, MO, US); *Wetmore & Abbe 116* (A, F, GH, MO), *116A* (A). COLÓN: Trail along first river W of Portobelo, *Gentry 5135* (MO). Near María Chiquita, *Gentry 6300* (MO). PANAMÁ: Moist woods, Río Tapia, *Standley 30675* (A, MO, US).

11. **Zanthoxylum pittieri** P. Wilson in Pittier, Contr. U.S. Natl. Herb. 20: 479. 1922. TYPE: Panama, *Pittier 5713* (US, holotype; NY, isotype).

Trees, ca. 20 m high; trunks armed, the branchlets armed. *Leaves* even-pinnate, ca. 30 cm long; petiole and rachis scabridulous; leaflets 8, alternate, oblong or oval to ovate or obovate, rounded and with a short broad acumination apically, inequilateral and rounded basally, the margins entire and revolute, the blade pellucid punctate throughout, coriaceous, scabridulous on both sides, 7.5–13.0 cm long, 57–80 mm wide, the petiolules 6–8 mm long. *Staminate panicles* axillary, widely and sparsely branched, ca. 25 cm long, the branches tomentulose with reddish trichomes. *Staminate flowers* white, apparently glabrous, the pedicels less than 1 mm long; calyx 5-lobed, ca. 1 mm high, the lobes obtuse; petals 5, ovate, imbricate, ca. 2 mm long, 1 mm high; stamens 5, ca. 2 mm long; disc 5-lobed, 10-sulcate; carpels 3, rudimentary. *Carpellate flowers* and *fruits* unknown.

This species is known only from the type collection, flowering in February. *Zanthoxylum pittieri* occurs in monsoon forest. It is easily recognized by the reddish tomentulose inflorescences.

DARIÉN: Boca de Pavarandó on the Río Sambú, 20 m, *Pittier 5713* (NY).

12. **Zanthoxylum procerum** Donnell Smith, Bot. Gaz. 23: 4. 1897.—Fig. 8. SYNTYPES: Costa Rica, *Tonduz 2348, 9920; Donnell Smith 6469* (all F?, none seen).

Trees, 4.5–15.0 m high; trunks armed with basally rounded prickles, the branches armed with short prickles, the branchlets glandular punctate and with numerous minute peltate scales, minutely puberulent, becoming glabrate. *Leaves* even-pinnate, 5.5–71.5 cm long; petiole and rachis glandular punctate and with numerous minute peltate scales, rarely armed with small brownish prickles; leaflets (2–)6–16, opposite, narrowly elliptic to ovate or obovate, abruptly acuminate apically, acute, slightly inequilateral and decurrent basally, the margins crenulate and revolute, the blade pellucid punctate only marginally at the bases of the crenations, with numerous minute peltate scales on both the surfaces, 7.5–21.0 cm long, 23–72 mm wide, the petiolules 5–9 mm long. *Staminate panicles* corymbose, axillary or terminal, highly branched, spreading, to 13 cm long, the

branches minutely puberulent, glandular punctate and with numerous minute peltate scales. *Staminate flowers* white; calyx 3-lobed, the lobes triangular, obtuse; petals 3, elliptic, ca. 2 mm long, 1 mm wide; stamens 3, exserted, 3 mm long; ovary ovoid, less than 1 mm in diameter, the styles connate, less than 1 mm long. *Carpellate panicles* corymbose, axillary or terminal, spreading, 12.0–19.5 cm long, crowded at the ends of the branches. *Carpellate flowers* with the pedicels ca. 1 mm long in fruit; calyx 3-lobed, the lobes triangular, acute, less than 1 mm long. *Follicles* 1, globose, brownish, glandular punctate, densely covered with minute peltate scales, 5 mm long, short stipitate; seeds globose, purplish black, minutely dotted, 3 mm in diameter.

This species ranges from southern Mexico to Panama. In Panama, it is known to flower in February, March, and May and to fruit in March and June through September.

Zanthoxylum procerum is a species of monsoon forest, evergreen seasonal forest, and cloud forest. Unlike *Z. belizense*, *Z. panamense*, and *Z. setulosum*, the other widespread species on the Isthmus, it appears to occur with equal frequency on both sides of the Continental Divide. Common names reported for *Z. procerum* are: alcabú (*Cooper & Slater 162, 231*; *Duke 10254*); ikor (*Duke 14457*); and lagarto (*Cooper & Slater 231*). There are many comments on herbarium labels on the strong odor of leaves, flowers, fruits, and cut wood.

CANAL ZONE: Pipeline Road, *Correa A. & Haines 535* (MO); *Croat 12758* (MO, SCZ). Maru Towers, *Johnston 1715* (A, MO). Pipeline Road, *Lao et al. 23* (MO). Between Ft. Davis and Coco Solo Hospital, *Tyson 6811* (MO). BARRO COLORADO ISLAND: *Croat 5847* (MO), *11670, 12189* (both MO, SCZ), *17372* (MO); *Ebinger 24* (MO, US); *Foster 1785* (DUKE); *Shattuck 16, 1137* (both F, MO); *Standley 31437* (US). CHIRIQUÍ: Progreso, *Cooper & Slater 162* (A, F, GH, NY, US), *231* (F, NY, US). DARIÉN: Near Refugio, 15–21 mi N of Santa Fé, 30 m, *Duke 10254* (MO). PANAMÁ: Cloud forest above Su Lin Motel, *Croat 14747* (MO). Cerro Campana, *D'Arcy 5500* (MO); *Dressler 4024* (MO). Between Cañazas and Sábalo, ca. 100 m, *Duke 14457* (MO). VERAGUAS: 1.5 km S of Escuela Agrícola Alto de Piedra, *Mori & Kallunki 5312* (MO).

13. **Zanthoxylum pucro** D. M. Porter, J. Arnold Arbor. 53: 406. 1972. TYPE: Panama, *Duke 13029* (MO, holotype; GH, isotype).

Trees; trunks armed, the branchlets glabrous. *Leaves* apparently odd-pinnate; petiole and rachis more or less canaliculate above, glabrous, together, 44.0–53.5 cm long; leaflets apparently alternate, oblong, abruptly acuminate apically, oblique and inequilateral basally, the margins crenate, the blade pellucid punctate only at the bases of the crenations, membranaceous, glabrous, 6.5–17.5 cm long, 3–6 cm wide, the petiolules winged, to 5 mm long. *Staminate panicles* terminal(?), congested, the branchlets scabridulous. *Staminate flowers* green in bud, the pedicels to 1 mm long, scabridulous; sepals 5, broadly triangular, glandular punctate, the margins hyaline, ciliate, ca. 1 mm long, the outer 3 larger; petals 5, obovate, glandular punctate; stamens 5; ovary ovoid, sharply 5-lobed and each lobe bilobed, glandular punctate, glabrous, star shaped in cross section, less than 1 mm in diameter, the styles 3, free. *Carpellate flowers* and *follicles* unknown.

This species is known only from the type collection, flowering in June.

DARIÉN: Forest 1–4 mi N of Pucro, *Duke 13029* (GH, MO).

14. **Zanthoxylum scheryi** Lundell in Woodson & Schery, Ann. Missouri Bot. Gard. 28: 481. 1941. TYPE: Panama, *Woodson & Schery 451* (MICH, holotype, not seen; GH, MO, isotypes).

Trees or *shrubs*, 1.5–10.0 m high; trunks armed with short prickles, the branchlets brownish, younger parts covered with minute golden glandular trichomes, becoming glabrate. *Leaves* odd- or even-pinnate, 18.5–31.0 cm long; petiole 3–6 cm long, petiole and rachis canaliculate above, minutely puberulent in the sulcus; leaflets (3–)7–9(–10), opposite to subopposite, elliptic or oblong to obovate, acute to obtuse and retuse to occasionally emarginate apically, acute and decurrent basally, the margins entire and revolute, the blade pellucid punctate marginally and with many small impressed punctations on both the surfaces, subcoriaceous, usually minutely puberulent above along the impressed midrib, the midrib conspicuous beneath, 16–85(–120) mm long, 13–40(–45) mm wide, the petiolules canaliculate, 2–23 mm long, those of the terminal leaflets longest. *Staminate panicles* corymbose, axillary, solitary, minutely puberulent and with minute golden glandular trichomes, to 18 cm long. *Staminate flowers* greenish yellow, the pedicels minutely puberulent, 1.5–2.0 mm long; sepals 5, connate basally, triangular, acute, spreading, less than 1 mm long, the outer 3 larger; petals 5, oblong lanceolate, spreading, keeled dorsally, 3 mm long; stamens 5, to 3 mm long; ovary 5-lobed, rudimentary, the styles connate, less than 1 mm long. *Carpellate panicles* axillary, minutely puberulent, with orange or red glandular trichomes especially common on the pedicels, 8–12 cm long in fruit. *Carpellate flowers* greenish, the pedicels 4–5 mm long in fruit. *Follicles* 1–4, red at maturity, subglobose, sparsely and minutely puberulent and with minute golden glandular trichomes, 6–7 mm in diameter, the stipe 2–3 mm long.

This species occurs in Panama and Costa Rica. In Panama, it is known to flower in July and August and to fruit in July and September. This species and *Z. melanostictum* are closely related. Further study perhaps will show them to be conspecific. *Z. scheryi* is known as arcabú or tachuelo (fide *Lao 396*).

CHIRIQUÍ: 2.2 km SW of Cerro Punta on road above IDAAN water tank, 2100–2250 m, *Croat 26309* (MO). E of Boquete on Cerro Azul near Quebrada Jaramillo, 1500–1600 m, *Croat 26806* (MO). Road up E slope of Volcán Barú, 10 mi from Boquete, 2500 m, *Croat 34977* (MO). Las Cumbres, hogback ridge N of Quebrada Iglesia, *Croat & Porter 16069, 16070* (both MO). Cerro Punta, 2000 m, *Lao 396* (MO). E side of Volcán Barú, road from Boquete to near summit, 2500 m, *Mori & Bolton 7414* (MO). Potrero Muleto to summit, Volcán de Chiriquí, 3500–4000 m, *Woodson & Schery 451* (GH, MO).

15. **Zanthoxylum setulosum** P. Wilson in Pittier, Contr. U.S. Natl. Herb. 20: 480. 1922.—Fig. 9. TYPE: Panama, *Pittier 3515* (US, holotype; NY, US, isotypes).

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FIGURE 9. *Zanthoxylum setulosum* P. Wilson—A. Habit (×½).—B. Fruit (×4). [After *Stern et al. 167* (MO).]

B
A
L. Mounick

Trees, 3–20 m high; trunks usually armed with numerous vertically flattened prickles, the branchlets hispidulous, becoming glabrate, usually armed with small sharp prickles. *Leaves* odd- or rarely even-pinnate, usually conspicuously yellowish pubescent, especially below, 25–68 cm long; petiole and rachis sometimes armed with scattered yellowish prickles, more or less canaliculate above, hispidulous and strigillose; leaflets 15–27, subopposite, elliptic to lanceolate or rarely ovate or obovate, acute and long acuminate apically, inequilateral and more or less acute basally, the margins crenulate and revolute, the blade pellucid punctate throughout, subcoriaceous, strigose above, the midvein hispidulous, paler and hispidulous beneath, especially on the veins, rarely with a few yellowish prickles on the midvein beneath, 3.0–13.5 cm long, 18–57 mm wide, the laterals more or less subsessile, the terminals petiolulate. *Staminate panicles* axillary and subterminal, congested, to 7 cm long, the branches hispidulous to villose. *Staminate flowers* yellow, the pedicels less than 1 mm long; calyx 5-lobed, less than 1 mm high, the lobes rounded, pubescent; petals 5, elliptic, 1.5–2.0 mm long; stamens 5, exserted, ca. 3 mm long; ovary 1–4-lobed, rudimentary, the styles 1–4. *Carpellate panicles* axillary, few- to many-branched, 3.5–16.0 cm long, the branches hispidulous to villose to almost glabrate, several often clustered together subapically on a branch to form a compact globose mass. *Carpellate flowers* with the pedicels less than 1 mm long; calyx 5-lobed, less than 1 mm high; lobes triangular, acute, pubescent; carpels 5, free. *Follicles* 1–4(–5), globose, brown, roughened with black or brownish punctations, glabrous, ca. 3 mm in diameter; seeds globose, dark brown to black, lustrous, minutely pitted, 2.5 mm in diameter.

This species occurs in Panama and Costa Rica, and it is known to flower in April and to fruit in March through October and in December.

Zanthoxylum setulosum, the most widespread and common species of its genus on the Isthmus, has not been collected in the western third of Panama. It occurs in monsoon forest, mainly on the Pacific side of the Continental Divide. Leaves on young specimens are extremely prickly, more crenate, often less pubescent, and have more pellucid punctations than those of mature individuals. The stems of *Erlanson 285* were noted as "hollow and filled with ants." Johnston (1949) has pertinent comments on the morphology of this species, and on its ability to spread into disturbed habitats. It is known as prickle yellow (*Bartlett & Lasser 16550*) in English, and as acabu, alcabu, or arcabu in Spanish, common names also applied to *Z. panamense* and other species.

CANAL ZONE: Woods on Canal Zone boundary near Juan Mina, *Bartlett & Lasser 16550* (DUKE, MO). Old road to Gamboa between Madden Wye and Summit Radio Station, *Croat 15019* (MO). Across road from Summit Hills Golf and Country Club, *Croat 17056* (MO). Pipeline Road 3 mi NW of Gamboa, *Haines 563* (DUKE, MO). Moist thicket, Darien Station. *Standley 31598* (US). Curundu Survival School Area, *Tyson & Dwyer 4461* (MO, SCZ). Bank of Río Cocolí, Miraflores Lake, *White 162* (MO). BARRO COLORADO ISLAND: *Croat 5430. 9043* (both MO, SCZ), *11261, 13924* (both MO); *Foster 848* (DUKE, MO); *Kenoyer 671* (US); *Oppenheimer 66-8-16-1542* (MO). COCLÉ: La Pintada, ca. 300 m, *Allen 3608* (GH, MO, NY, US). DARIÉN: Río Pirre, *Croat & Porter 15527* (MO). Just S of El Real, *Duke 5032* (MO). Santa Fé, *Duke 8409* (MO). 1–3 km S of El Real near sea level, *Gentry 13468* (MO). Pinogana, *Pittier 6570* (GH, US). El Punteado, Interamerican Highway bridge downstream from Yaviza along Río Chucunaque, *Stern et al. 167* (GH, MO, US). Othon's pasture S of El Real, *Stern et al. 744* (GH, MO, US). HERRERA: La Cabuya, 350 m, *Lao 137* (MO). LOS

SANTOS: Las Tablas, *Dwyer 1162* (MO). PANAMÁ: Cerro Azul, *Croat 17318* (MO). Gallery along Río Mamoní, *Duke 5688* (MO). San Jose Island, Bald Hill, *Erlanson 285* (GH, US). Between Red Hill and East Bay, *Johnston 150* (GH, MO, US). North Loop Road, *Johnston 623* (GH). South Road near fork to Naval Station, *Johnston 737* (GH, MO, US). Camp Valley E of Main Beach, *Johnston 795* (GH, MO, US). Loop at Little Butch, *Johnston 915* (GH). Río Chagres above Alajuela, *Pittier 3515* (NY, US). Near big swamp E of Río Tocumen, *Standley 26555* (US). Río Tapía, *Standley 38233, 28302* (both US). Juan Diaz, *Standley 30507, 30604* (both US). Río Tapía, *Standley 30663* (US). Nuevo San Francisco, *Standley 30705* (US). Between Las Sabanas and Matías Hernández, *Standley 31883* (US). Ensenada La Bodega, *Stimson 5320* (DUKE, MO, NY, SCZ). 2 mi E of El Llano, *Tyson 1736* (MO, SCZ, US).

16. **Zanthoxylum tripetalum** (Standley) D. M. Porter, Ann. Missouri Bot. Gard. 58: 261. 1972.

Amyris tripetala Standley, Field Mus. Nat. Hist., Bot. Ser. 22: 84. 1940. TYPE: Panama, *Davidson 621* (F, holotype; GH, MO, US, isotypes).

Small *trees* 3–6 m high; trunks usually armed with conical prickles. *Leaves* odd-pinnate, to 11 cm long; petiole glabrous, 11–18 mm long; leaflets (3–)5–7, opposite, unequal, narrowly elliptic, obtuse and long attenuate apically, attenuate basally, the margins obscurely crenulate, the blade pellucid punctate only marginally at the bases of the crenulations, with minute peltate scales on both surfaces, 22–72 mm long, 8–18 mm wide, subsessile or the petiolules to 3 mm long. *Staminate panicles*, corymbose, axillary or terminal, spreading, to 7 cm long, 10 cm wide. *Staminate flowers* creamy white, the pedicels to ca. 1.5 mm long; sepals 3, ovate triangular, apiculate, less than 1 mm long; petals 3, ovate elliptic, keeled dorsally, 2.0–2.5 mm long, ca. 1 mm wide; stamens 3, exserted, 3.0–3.5 mm long; ovary 3-lobed, glabrous, less than 1 mm in diameter, the styles connate. *Carpellate flowers* and *follicles* unknown.

Zanthoxylum tripetalum is endemic to Panama. It is known to flower in April and May.

CHIRIQUÍ: Boquete, 3800 ft, *Davidson 621* (F, GH, MO, US). Denuded premontane rain forest between Pinola and Quebrada Seco on Chiriquicito-Caldera Trail, *Kirkbride & Duke 1024* (MO).

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FLORA OF PANAMA[1]

BY ROBERT E. WOODSON, JR. AND ROBERT W. SCHERY
AND COLLABORATORS

Part VIII

FAMILY 156. STYRACACEAE

W. G. D'ARCY[2]

Trees or *shrubs* of spreading habit, stellate pubescent to glabrous, sometimes lepidote. *Leaves* alternate, entire, serrate or denticulate, often glabrous above and pubescent or lepidote beneath, estipulate. *Inflorescences* simple or sparingly branched racemes, axillary or terminal, sometimes corymbose or reduced; pedicels subtended by reduced foliose bracts. *Flowers* with the calyx synsepalous, truncate or 4–5-lobed, the lobes mostly small, the corolla egress often stretching the calyx apex into a thin sleeve; corolla mostly white, campanulate or tubular, 4–5-lobed or divided, valvate or imbricate; stamens in one whorl, rarely as many as the petals, mostly twice as many, sometimes in 2 alternating series, the filaments basally connate, the tube adnate to the corolla, sometimes extending above it, glabrous or pubescent, the anthers narrow, basifixed, sometimes versatile, dehiscing longitudinally, introrse; ovary superior or inferior, of 3–5 fused carpels, mostly basally 3–5 locular and apically 1-locular by virtue of the basal septation and the axile placenta; ovules 1–many in each locule, erect or pendulous, anatropous, tenuinucellate, the style terminal, united, the stigma punctiform or minutely 3–5 lobate. *Fruit* a capsule or drupe, sometimes baccate, sometimes winged; seeds 1–many, often 1–few by abortion, embryo straight or slightly curved, the cotyledons appressed, the endosperm present.

Literature:

De Candolle, A. 1844. Styracaceae *in* A. P. De Candolle. Prodromus Systematis Naturalis 8: 244–272.

Gonsoulin, G. J. 1974. A revision of *Styrax* (Styracaceae) in North America, Central America, and the Caribbean. Sida 5: 191–258.

Metcalfe, C. R. & L. Chalk. 1950. Anatomy of the Dicotyledons. Oxford.

Perkins, J. 1907. Styracaceae *in* A. Engler, Das Pflanzenreich IV(241): 1–111.

Schadel, W. E. & W. C. Dickison. 1979. Leaf anatomy and venation patterns of the Styracaceae. J. Arnold Arboretum 59: 8–37.

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[1] Assisted by National Science Foundation Grant DEB 77-04300 (William G. D'Arcy, principal investigator).

[2] Missouri Botanical Garden, 2345 Tower Grove Avenue, St. Louis, Missouri 63110.

ANN. MISSOURI BOT. GARD. 66: 165–172. 1979.

0026-6493/79/0165–0172/$00.85/0

1. STYRAX

Styrax L.,[3] Sp. Pl. 444. 1753; Gen. Pl., ed. 5. 203. 1754. TYPE: *S. officinalis* L.

Strigilia Cav., Diss. 7: 383, t. 8. 201. 1789. TYPE: *S. racemosa* Cav. = *Styrax racemosus* (Cav.) A. DC.

Shrubs or *trees* of spreading habit, stellate pubescent, lepidote or glabrate. *Leaves* alternate, entire or sometimes minutely serrate, mostly glabrous above and tomentose or lepidote beneath, estipulate. *Inflorescences* axillary or terminal, mostly short, lax racemes, small bracts subtending the pedicels. *Flowers* with the calyx mostly cupular, truncate or minutely 4–5 dentate, sometimes basally adnate to the ovary, stellate pubescent or lepidote; corolla mostly white, 5(–6–7) parted about ½ down or more, the lobes valvate or imbricate, mostly narrow, pubescent or lepidote dorsally; stamens 10(8–13), the filaments flat, basally united into a tube which is adnate to the corolla tube, the anthers narrow, the locules linear, parallel, dehiscing longitudinally; ovary mostly superior, ovoid, globose, depressed or minutely stipitate, mostly pubescent, 3-locular basally, 1-locular above, the ovules 1–few in each locule, the style slender, the stigma minute. *Fruit* an ovate, elliptical or globose drupe or a dry, sometimes valvate, dehiscent capsule; seeds 1–2 by abortion.

Styrax includes about 130 species widely distributed in temperate and tropical regions. The gum of several species is used for making incense and species are sometimes cultivated for ornament in temperate regions. The name "storax" or "estoraque" is applied to trees of this genus and to *Liquidambar styraciflua* L. (Hamamelidaceae, not in Panama). It is also applied to the gum of the European *Styrax officinalis* L. The same name and "estoraque liquido" is applied to the gum of *Liquidambar styraciflua* L. Gum benzoin or "benjui" is obtained from *Styrax benzoin* L. of Southeast Asia and it is sometimes used in medicine. The plants are pubescent or lepidote on nearly all parts except the tops of the leaves and the indumentum of the Panamian species is a stellate tomentum. Recognition is further facilitated by the 1–2 seeded drupe and 10 stamens.

Species of *Styrax* are often difficult to separate, at least in the herbarium, and distinctions often rest on niceties of indumentum and leaf shape or texture. Perkins (1907), who monographed the genus for the world, recognized many variants of minor detail which Gonsoulin (1975) in his treatment of North and Central American species reduced to a few species. The treatment presented here rests heavily on Gonsoulin's concepts. Few types were seen, and Gonsoulin unfortunately did not indicate whether he saw types himself.

Styrax is the Greek name for *Styrax officinalis*, and as a shrub it was treated by most ancient writers as masculine, but by a few as feminine. Transliterated into botanical Latin, it was treated as feminine by pre-Linnaean authors. But Linnaeus published the species known to him with a neuter ending, *S. officinale*. Because he added no text which might confirm his intentions, it is assumed that this was a grammatical error which should be corrected to the feminine *S. of-*

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[3] For a list of synonyms see Gonsoulin (1974). Only the names noted here have been used for Panamanian plants.

ficinalis. Practice by subsequent botanists has varied, thus A. De Candolle (1844) treated the genus as neuter, Perkins (1907) treated it as feminine, and Gonsoulin (1974) presented the species with a mixture of generic endings. Major current texts in North America and Europe treat the genus as feminine, although practice is not uniform. For a discussion of classical application of gender to this name, see Nicolson & Steyskal (1976). They concur that the name should not be neuter, but argue that masculine instead of feminine should be used. The question is far from settled: recently Maguire & Huang (1978) accepted the position taken here by treating *Styrax* as feminine, although they maintained one species in the original masculine of its authors.

Literature:

Maguire, B. & Yung-Chau Huang. 1978. Styracaceae *in* The Botany of the Guayana Highland Part X. Mem. N.Y. Bot. Gard. 29: 204–223.

Nicolson, D. H. & G. C. Steyskal. 1976. The masculine gender of the generic name *Styrax* Linnaeus (Styracaceae). Taxon 25: 581–587.

a. Indumentum of stellate hairs, the arms free or united only at the base; leaves glabrous above ——— 1. *S. argenteus*

aa. Indumentum of peltate scales formed of hairs with the arms united to the tips (scutellate); leaves with dispersed scales above ——— 2. *S. conterminus*

1. **Styrax argenteus** Presl., Reliq. Haenk. 2: 60. 1836. TYPE: Acapulco, Mexico, *Haenke* (?PR, not seen; isotype MO).—FIG. 1.

Small *tree* to 12 m tall, the twigs slightly angled, soon terete, tomentose on emerging, soon only the tightly appressed elements remaining and thus appearing glabrous. *Leaves* ovate or elliptical, to 12(–18) cm long, 6(–11) cm wide, apically acuminate, basally obtuse or rounded, entire, glabrous above, whitish tomentose beneath with stellate hairs, the indumentum appressed or lax, veins impressed above, elevated and often rufous beneath, lateral veins 6–8 on each side, nearly straight and ascending, ultimately arcuate, the minor venation evident or not; petiole 12–18 mm long, mostly tomentose, drying angled beneath. *Inflorescences* short lax racemes to 8 cm long, slightly congested, the peduncle grayish or brownish, fine tomentose, angled; bracts ca. 1 mm long, narrow, scalelike, caducous; pedicels 8–10 mm long, evenly fine tomentose, angled. *Flowers* with the calyx cupular, ca. 4 mm long and wide, subtruncate with 5 minute umbos, thinned apically into a sleeve, finely and evenly stellate tomentose outside, inside minutely appressed pubescent with ascending, reduced hairs; corolla white, often drying pale purplish, ca. 15 mm long, divided to the calyx rim into narrow segments, evenly pubescent outside, valvate in bud; stamens 10, the filaments ca. 7 mm long, basally united into a tube for 3–4 mm, the tube adnate to the corolla base for ca. 2 mm, ventrally glabrous, dorsally fine tomentose, ciliate and densely tufted just above the point of insertion, the anthers linear, exserted from the corolla tube but slightly shorter than the lobes, the connective covering the back, the thecae discrete, stellate pubescent; ovary ovoid, apiculate, evenly fine tomentose overall and on the apicule with stellate hairs, the style slender, the stigma

FIGURE 1. *Styrax argenteus* Presl.—A. Flowering branch (×½). [After *Gentry & Mori 13797* (MO.]—B. Fruiting branch (×½). [After *Allen 4851* (MO).]

minutely 3-lobed. *Fruit* an ellipsoidal or obovate drupe, ca. 2 cm long, finely tomentose; seed 1.

Styrax argenteus ranges from Mexico (Sinaloa) south through Central America to at least as far as Peru. It is easily distinguishable from the other Panamanian species by its stellate hairs which may be appressed or ascending, or a mixture of both. It is distinguished from other species of *Styrax* by its acuminate leaves, stellate pubescence and elongate fruit. A number of other species of South

America are closely related, e.g., S. *guianensis* A. DC. from northeastern areas and S. *oblongus* (R. & P.) A. DC. from Peru.

Gonsoulin distinguished three varieties in S. *argenteus*, two of them occurring in Panama. The distinctions between them are not always evident without close attention to trichome structure, and the separation may not be taxonomically useful. Some collections are intermediate. Gonsoulin did find a geographic basis for recognizing the two varieties, noting that var. *argenteus* is more typically northern whereas var. *micranthus* (var. *ramirezii* of Gonsoulin) is more typical of Costa Rica, Panama, and other southern parts of the range.

In Panama, *Styrax argenteus* has been most commonly collected from Chiriqui Province from 1200–2800 m, but one Chiriqui collection was taken at only 870 m, and the collections from Cocle and Colon are from below 350 m. In Mexico this species is called Chucamaya.

a. Tomentum of leaf undersides loose, the hairs larger, the arms ascending, free from one another and sometimes appearing to come off the axis at slightly different levels ..... 1a. var. *argenteus*

aa. Tomentum of leaf undersides appressed, the hairs minute, close, the arms mostly porrect, sometimes connate centrally ..... 1b. var. *micranthus*

1a. **Styrax argenteus** Presl. var. **argenteus.**

Strigilis argenteus (Presl.) Miers, Ann. Mag. Nat. Hist. ser. 3. 3: 282. 1859.
Styrax punctatum sensu Donnell Smith, Enum. Pl. Guatem. 2: 46. 1891; 4: 104. 1895, non DC.
S. *myristicifolius* Perk., Bot. Jahrb. Syst. 31: 481. 1902. SYNTYPES: Veraguas, Panamá, *Warscewicz* 2, not seen; Guatemala, *Heyde & Lux 6182*, not seen.

Material of this variety is identified in the following specimen citations by an asterisk.

1b. **Styrax argenteus** var. **micranthus** (Perk.) D'Arcy, comb. nov.

S. *ramirezii* Greenman, Proc. Amer. Acad. Arts 34: 568. 1899. SYNTYPE: Mexico, *Pringle 6848* (US, MO).
S. *polyanthus* Perk., Bot. Jahrb. Syst. 31: 479. 1902. LECTOTYPE: Guatemala, *Donnell Smith 2266* (US).
S. *micranthus* Perk., Bot. Jahrb. Syst. 31: 480. 1902. TYPE: Mexico, *Ehrenberg 498* (not seen).
S. *warscewiczii* Perk., Bot. Jahrb. Syst. 31: 480. 1902. TYPE: Veragua, Panamá, *Warscewicz 203* (B, if extant, not seen; photo MO).
S. *polyneuris* Perk., Bot. Gaz. (Crawfordsville) 35: 5. 1903. TYPE: Costa Rica, *Tonduz 11744* (CR, not seen).
S. *cyathocalyx* Perk., Feddes Repert. 2: 24. 1906. TYPE: Oaxaca, Mexico, *Galeotti 1687* (not seen).
S. *orizabensis* Perk., Feddes Repert. 2: 25. 1906. TYPE: Mexico, *Botteri 1006* (B, G-DC, W, none seen).
S. *ramirezii* var. *micranthus* (Perk.) Perk., Pflanzenreich IV 4(241): 54. 1907.
S. *ramirezii* var. *orizabensis* (Perk.) Perk., Pflanzenreich IV 4(241): 54. 1907.
S. *panamensis* Standley, Contr. U.S. Natl. Herb. 18: 121. 1916. TYPE: Panamá, *Pittier 4242* (US, holotype; NY, US, isotypes).
S. *argenteus* var. *ramirezii* (Greenm.) Gonsoulin, Sida 5: 227. 1974.

CHIRIQUÍ: Road to Bambito, 4500 ft, *Allen 4851* (F, MO, NY, US). 10 mi above Boquete on road to Volcán Barú, 2600 m, *Croat 34830** (MO); 2500 m, *Croat 34981* (MO). El Barú above Boquete, 1200–1800 m, *D'Arcy 9887** (MO). Alto Respinga and above, ca. 3800 m, *D'Arcy 9992** (MO). E slope of Volcán de Chiriquí WNW of Boquete, 1900–2000 m, *Davidse & D'Arcy 10164** (MO); 2400 m, *Davidse & D'Arcy 10216* (MO). Boquete, 5500 ft, *Davidson*

776 (F, MO, US); *Dwyer 7006* (MO). Boquete, Fred Collins Finca, *Ebinger 716** (MO). W side of Volcán Barú, 2000–2500 m, *Mori & Bolten 7359* (MO). E side of Volcán Barú, 2500 m, *Mori & Bolten 7416* (MO). Boquete, Finca Collins, 5800–6700 ft, *Stern et al. 1993* (MO), *2045** (MO, US). Camiseta, Volcán de Chiriquí, Boquete District, 7500 ft, *Terry 1338** (F, MO). Volcán de Chiriquí, 9000 ft, *Terry 1348** (F, MO). Canyon bottom 6 mi NE of El Volcán, 74–7500 ft, *Tyson 826, 827a* (both MO). 8 mi N of Concepción, 2900 ft, *Webster 16616* (DAV). Río Chiriquí Viejo valley, *White 70* (F, MO, US). Callejon Seco, Volcán de Chiriquí, 1700 m, *Woodson & Schery 484* (F, MO). Casita Alta, Volcán de Chiriquí, 1500–2000 m, *Woodson et al. 919* (F, MO, NY). COCLÉ: Olá, 100–350 m, *Pittier 5076** (NY, US). COLÓN: Loma de Gloria near Fató, 10–104 m, *Pittier 4242* (NY, US). DARIÉN: Cerro Tacarcuna summit camp, 1550–1650 m, *Gentry & Mori 14073** (MO). Cerro Mali base camp near Colombian border, 1500 m, *Gentry & Mori 13797** (MO).

2. **Styrax conterminus** Donnell Smith, Bot. Gaz. (Crawfordsville) 18: 5. 1893.

TYPE: Guatemala, *Heyde & Lux 2915* (MO, isotype).

Tree 5(–14) m tall, the twigs sharply angled, somewhat rufous with scutellate, peltate scales. *Leaves* oblong or elliptical, 5–17 cm long, 3–5 cm wide, subcoriaceous, apically acuminate, basally obtuse, the veins 6–9 on each side, arcuate, impressed above, elevated and somewhat rufous beneath, the minor venation reticulate, sometimes indistinct, the minor venation minutely elevated on each side, appearing glabrous above but with dispersed peltate scutellate scales 0.3 mm across, beneath fine appressed tomentose with white scutellate scales and punctate with emergent, darker scales; petiole 8–20 mm long, slender, lepidote. *Inflorescences* short racemes to ca. 5 cm long in the axils of the upper leaves; peduncle angled, slender; pedicels nodding, angled, 7–10 mm long; bracts scale-like, ca. 2 mm long, caducous. *Flowers* 10–14 mm long, calyx finely and evenly lepidote, subtruncate, cupular, 3–4 mm long and about as wide; corolla valvate, divided to the calyx rim into linear segments, dorsally fine tomentose, 7–9 mm long; stamens 10, the filaments connate for the basal ⅔, adnate to the corolla tube for the basal ½, appressed pubescent dorsally, with a prominent inconspicuously tomentose boss on the ventral side just above the point of corolla insertion, glabrous and narrower above, the anthers linear, 2-thecate, exserted from the corolla tube but shorter than the corolla lobes, the connective covering the back of the anther; ovary apically subtruncate, beaked, scutellate-lepidote overall, the stigma linear with 3 minute stigmatic lobes, slightly exceeding the anthers. *Fruit* not seen (Gonsoulin), 12–15 mm long, 7–8 mm wide, silvery lepidote; seed usually 1.

This species is distinguished from the other Panamanian species of *Styrax* by its indumentum which is visible under a hand lens. The arms of the stellae are fused for most of their length into scutellate scales, and the scale is peltate or subsessile. In some areas such as leaf undersides, the scales form a dense, fine, closed tomentum.

Styrax conterminus is perhaps conspecific with S. *ovatus* (R. & P.) A. DC. from Peru, but it was treated as separate by both Perkins and Gonsoulin. The photograph of the type collection from Berlin reveals a plant with somewhat wider leaves and perhaps more ample inflorescences which may token a different species. No collections of S. *ovatus* were seen from Peru. *Styrax conterminus* is

the only species of *Styrax* in Central America with a scutellate indumentum. Three other such species occur in the Antilles and more than one other may occur in South America. The species is known in Panama only by one collection from western Chiriqui.

CHIRIQUÍ: Cerro Colorado along mining road 31.6 km beyond Río San Félix, 1690 m, *Croat 37190* (MO).

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FLORA OF PANAMA[1]

BY ROBERT E. WOODSON, JR. AND ROBERT W. SCHERY
AND COLLABORATORS

Part IX

FAMILY 171. SCROPHULARIACEAE

W. G. D'ARCY[2]

Mostly *herbs* or *shrubs*, rarely *trees* or *lianas*, sometimes paludal or aquatic, sometimes parasitic or saprophytic, glabrous or pubescent with simple or branched, glandular or eglandular hairs, often gland dotted, often drying black. *Leaves* opposite or alternate, occasionally verticillate, simple or compound, mostly serrate to denticulate, sometimes deeply incised; exstipulate. *Inflorescences* cymose, racemose or spicate, often with flowers solitary or in pairs, mostly axillary; pedicels mostly subtended by 1–2 bracts, the bractlets sometimes present, the bracts sometimes colorful. *Flowers* mostly perfect, zygomorphic, the calyx mostly of 5 similar or dissimilar, united or deeply divided lobes; corolla 5 or fewer lobed, mostly 2-lipped, the upper (posterior) lip of 3 lobes, often elaborated into saccate or other irregular forms; stamens (5)4 or 2, staminodes sometimes present, inserted in the corolla tube, mostly didynamous or 2, the anthers 1–2 thecate, the thecae sometimes separated on variously elaborated connective arms, sometimes confluent; disc sometimes present; ovary 2 locular at least basally, sometimes 1 locular apically, each locule with many(–few–1) anatropous or amphitropous ovules on elaborated placentas; styles mostly united, the stigmas 2 or 1. *Fruit* mostly a septicidal or also loculicidal capsule, sometimes a berry or nutlike, the placenta often persistent as a tuberculate peg, sometimes winged; seeds small, the embryo straight or slightly bent, the endosperm fleshy.

Literature:

Pennell, F. W. 1935. The Scrophulariaceae of Eastern Temperate North America. Acad. Nat. Sci. Philadelphia Monogr. 1: 1–650.

Standley, P. C. & L. O. Williams. 1973. Scrophulariaceae *in* Flora of Guatemala, Fieldiana, Bot. 24 (IX 3–4): 319–418.

Thieret, J. W. 1954. The tribes and genera of Central American Scrophulariaceae. Ceiba 4: 164–184.

———. 1967. Supraspecific classification in Scrophulariaceae: a review. Sida 3: 87–106.

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[1] Assisted by National Science Foundation Grant DEB77-04300 (W. G. D'Arcy, Principal Investigator).

[2] Missouri Botanical Garden, 2345 Tower Grove Avenue, St. Louis, Missouri 63110.

1. Leaves deeply lobed, dissected or compound.
   2. Plants submersed aquatics; leaves lax, the segments filiform ..... 5. *Benjaminia*

0026-6493/79/0173–0272/$10.05/0

2′. Plants terrestrial; leaves turgid or stiff, the segments linear to broad.
3. Corollas bright yellow, sometimes drying orange; calyces green, not showy; leaves membranaceous, the segments mostly more than 5 mm wide; corolla exserted, the lower lip inflated, entire ---- 7. *Calceolaria*
3′. Corollas green, red or yellowish; calyces or bracts red, often showy; leaves stiff, the segments mostly less than 3 mm wide; corolla included, the tube elongate, the lower lip 3-toothed ---- 9. *Castilleja*

1′. Leaves simple, toothed, crenate or entire, rarely lobed or dissected.
4. Fruit a globose capsule packed with hairs; corollas tubular, red or pink, glabrous outside, the flowers in clusters or pairs ---- 18. *Russelia*
4′. Fruit a capsule lacking internal hairs, or a berry; corollas various, if red and tubular then pubescent outside, flowers variously disposed.
5. Flowers more than 1.3 cm long.
6. Corollas bright yellow, sometimes drying orange; leaves lanceolate, petiolate ---- 7. *Calceolaria*
6′. Corollas red, white, greenish, sometimes fading yellowish; leaves various, if lanceolate, then sessile.
7. Flowers narrowly tubular or salverform.
8. Leaves mostly linear, mostly less than 4 mm wide; plants drying dark ---- 6. *Buchnera*
8′. Leaves more than 4 mm wide, ovate; plants drying green or brown.
9. Corolla salverform, the limb flaring, more than 3 cm wide; pedicels stout and elongate, bibracteate partway up ---- 11. *Escobedia*
9′. Corolla tubular, the limb mostly erect, less than 2 cm wide; pedicels either slender or short, lacking bracts.
10. Leaves entire; corolla glabrous outside, white or purplish ---- 12. *Gibsoniothamnus*
10′. Leaves dentate or serrate; corolla pubescent outside, red or orange ---- 13. *Lamourouxia*
7′. Flowers campanulate or irregular (saccate).
11. Leaves linear, less than 4 mm wide; plants drying dark ---- 1. *Agalinis*
11′. Leaves linear to ovate, more than 4 mm wide; plants mostly drying green or brown.
12. Leaves more than 2 cm wide; flowers white or pinkish.
13. Leaves opposite.
14. Leaves lanceolate; coarse herb mostly over 40 cm tall; fruit a rotund white berry ---- 14. *Leucocarpus*
14′. Leaves ovate; forest herb less than 30 cm tall; fruit a narrow capsule ---- 21. *Tetranema*
13′. Leaves alternate ---- 10. *Digitalis*
12′. Leaves less than 2 cm wide; flowers blue or purplish.
15. Capsule enclosed in the winged calyx cup; leaves ovate ---- 22. *Torenia*
15′. Capsule exserted from the short calyx cup; leaves linear ---- 3. *Angelonia*

5′. Flowers less than 1.3 cm long.
16. Leaves lanceolate, mostly over 2 cm wide, 10 cm long; large herbs mostly over 40 cm tall; fruit a white berry ---- 14. *Leucocarpus*
16′. Leaves various, if lanceolate then less than 2 cm wide, 10 cm long; herbs mostly less than 40 cm tall, or shrubs; fruit a capsule.
17. Capsule apically divided into 2 rounded lobes (Fig. 23.) ---- 23. *Veronica*
17′. Capsule unlobed, obtuse or globose.
18. Leaves linear, less than 5 mm wide and several times longer than wide, mostly entire, sometimes minutely and sparingly toothed.
19. Flowering calyx tubular; plants drying dark.
20. Corolla pink, purplish or white, the limb of spreading, subequal lobes; calyx green or dark, not showy; anthers 1-thecate ---- 6. *Buchnera*
20′. Corolla green or yellowish, the limb of unlike erect and recurved lobes; calyx showy red or orange; anthers 2-thecate ---- 9. *Castilleja*

19′. Flowering calyx either cup shaped, tubular, or leaflike; plants mostly not drying dark.
21. Calyx lobes of different size and shape, mostly ovate ..... 4. *Bacopa*
21′. Calyx lobes all alike, mostly narrow.
22. Flowers sessile or nearly so ..... 20. *Stemodia*
22′. Flowers distinctly pedicellate.
23. Fruiting pedicels less than 10 mm long; flowers white ..... 19. *Scoparia*
23′. Fruiting pedicels more than 10 mm long; flowers pink ..... 1. *Agalinis*

18′. Leaves deltoid, ovate, rotund or elliptic, mostly less than twice as long as broad (sometimes less than 5 mm wide), entire or toothed.
24. Leaves alternate; shrubs; corolla white, campanulate ..... 8. *Capraria*
24′. Leaves opposite; herbs; corolla white, yellow or blue, shapes various.
25. Leaves scabrous; flowers yellow, inconspicuous in spike-like terminal racemes ..... 2. *Alectra*
25′. Leaves smooth; flowers variously colored, pedunculate or sessile, solitary or in clusters.
26. Plants erect or ascending, mostly over 6 cm tall.
27. Placenta conspicuously winged by the septum after seeds have fallen; flowers blue or purplish.
28. Capsule enclosed in the calyx cup ..... 22. *Torenia*
28′. Capsule exserted from the calyx cup ..... 15. *Lindernia*
27′. Placenta peglike, globose or rudimentary, unwinged; flowers white or bluish.
29. Calyx lobes of different size and shape, mostly ovate or cordate.
30. Flowers yellow; anther cells separated on arms (Fig. 15.) ..... 16. *Mecardonia*
30′. Flowers white; anther cells contiguous, at least in part ..... 4. *Bacopa*
29′. Calyx lobes all alike, mostly narrow.
31. Capsules globose; flowers white ..... 19. *Scoparia*
31′. Capsules ovoid or ellipsoid; flowers blue ..... 20. *Stemodia*

26′. Plants prostrate, creeping, or ascending, less than 6 cm tall.
32. Fruits globose ..... 17. *Micranthemum*
32′. Fruits ovoid or ellipsoid.
33. Calyx lobes of different size and shape, mostly ovate or cordate.
34. Flowers yellow; anther cells separated on arms (Fig. 15.) ..... 16. *Mecardonia*
34′. Flowers white; anther cells contiguous, at least in part ..... 4. *Bacopa*
33′. Calyx lobes all alike, mostly narrow ..... 20. *Stemodia*

The Scrophulariaceae includes over 250 genera with over 5,000 species distributed worldwide, but with the greatest number of species in temperate regions. Many of the species are wide ranging.

The family can usually be recognized by the 2-lipped flowers with paired stamens and the conical or globose capsules which contain many small seeds

and a peglike placenta. There are many exceptions to these features, but the Scrophulariaceae has every appearance of being a natural group. However, some genera usually placed in the family may belong to other families. Thus Niezgoda and Tomb (1975) report that the pollen of *Capraria* is more like that in the Myoporaceae than in the Srrophulariaceae, and *Gibsoniothamnus* has characters strongly suggesting placement in the Bignoniaceae or Gesneriaceae rather than in the Scrophulariaceae. *Tetranema* is quite unlike other members of the Scrophulariaceae and is strongly suggestive of the Gesneriaceae. At the same time, *Nautilocalyx*, which is usually considered to belong to the Gesneriaceae, may actually belong to the Scrophulariaceae. At one time the Scrophulariaceae was considered to be closely related to the Solanaceae and some elements, e.g., *Verbascum* (not in Panama) were thought to be transitional between the two families. Several seemingly fundamental features, e.g., absence of internal phloem, presence of iridioid compounds, and regular rather than asymmetrical ovary placement argue against close affinity between these two large but somewhat similar families. The same features just noted support affinity of the Scrophulariaceae with the Bignoniaceae and Gesneriaceae.

Classification of the family tends to recognize two major groups, subfamily Scrophularioideae (Antirrhinoideae) in which the posterior (upper) lip of the corolla is external in bud, and subfamily Rhinanthoideae in which it is internal. The Rhinanthoideae are frequently parasitic and they have a greater tendency to dry dark. The greatest Panamanian development in the family is in tribe Gratioleae subfamily Scrophularioideae, which includes many paludal or aquatic herbs of both New and Old Worlds—in Panama: *Bacopa*, *Benjaminia*, *Capraria*, *Leucocarpus*, *Lindernia*, *Mecardonia*, *Micranthemum*, and *Stemodia*.

Many species of Scrophulariaceae are valuable horticultural items, especially in temperate gardens, and a few, e.g. *Digitalis*, yield drugs, but the family is of little economic importance.

1. AGALINIS

Agalinis Raf., New Fl. & Bot. N. Amer. 2: 61. 1837. (nomen cons. contra *Chyrta* Gaertn.). TYPE: *A. plustris* Raf. = *A. purpurea* (L.) Pennell (type cons.).

Chyrta Gaertn., Fruct. Sem. Pl. 3: 184. 1807. TYPE: *C. anomala* Gaertn. = *A. tenuifolia* (Vahl) Raf.

Virgularia Ruiz & Pavón, Fl. Peruv. Chile Prodr. 92, *tab. 19*. 1794. (nomen rejic. proposita). LECTOTYPE: *V. lanceolata* Ruiz & Pavón.

Tomanthera Raf., New Fl. Bot. N. Amer. 2: 65, *tab. 836*. 1837. TYPE: *T. lanceolata* Raf. = *Agalinis auriculata* (Michx.) Blake.

Otophylla Benth. in DC., Prodr. 10: 512. 1846. LECTOTYPE: *O. michauxii* Benth. = *Agalinis auriculata* (Michx.) Blake.

Anisantherina Pennell, Mem. Torrey Bot. Club 16: 106. 1920. Based on *Gerardia hispidula* Mart. = *Agalinis hispidula* (Mart.) D'Arcy.

Gerardia sensu auct., non L., Gen. Pl. ed. 5. 266. 1754. (nomen rejic. vs. *Stenandrium* Nees, Acanthaceae).

Herbs or *shrubs*, annual or perennial, usually erect, branched, virgate, glabrous hirsute or scabrous, eglandular; parasitic on the roots of other plants. *Leaves* opposite or alternate, often reduced upwards, mostly narrow, entire, glabrous

beneath, glabrous or scabrous above, lacking defined petioles. *Inflorescences* terminal racemes or panicles, mostly open; peduncles slender, often bracteate; pedicels bibracteolate or obsolete. *Flowers* mostly showy, pink, purple or sometimes white, the calyx tubular or campanulate, 5-lobed or toothed, the lobes sometimes denticulate; corolla campanulate, the tube straight or slightly curved, slightly inflated upwards, the limb spreading with 5 rounded lobes, sometimes somewhat 2-lipped; sometimes puberulent inside or out; stamens 4, didynamous, the filaments inserted halfway up the corolla tube, mostly pilose, the anther thecae equal or somewhat unequal but all similar in shape, mostly parallel, sometimes basally spurred, dehiscing longitudinally; ovary glabrous, 2-locular, the style slender, straight, deciduous, the stigma solitary, terminal. *Capsule* woody, chartaceous or sometimes leathery, mucronulate, loculicidally and sometimes septicidally dehiscent; seeds many, reticulate, oblong to prismatic.

Agalinis is usually easily recognized by its showy, distinct pink flowers and linear leaves on wiry stems. The name is used here in the hopes that the prior name, *Virgularia*, will be rejected by international committee. *Agalinis* includes about 40 species of the New World with the largest number of species (20) occurring in the eastern United States. *Agalinis* is closely related to *Sopubia*, a large Old World genus distinguished by having one anther sac reduced to a linear, fingerlike downward directed process. The name *Sopubia* Don. (1825) antedates *Agalinis*.

Literature:

D'Arcy, W. G. 1979. Proposal to conserve the name *Agalinis* Raf. (1837) against *Virgularia* Ruiż & Pavon (1794) Scrophulariaceae. Taxon 28: 419–422.

Hansen, O. J. 1975. The East African species of *Sopubia* (Scrophulariaceae). Kew Bull. 30: 543–558.

Pennell, F. W. 1928–29. 1929–30. *Agalinis* and allies in North America. Proc. Acad. Nat. Sci. Philadelphia 80: 339–449; 81: 111–247.

1. **Agalinis hispidula** (Mart.) D'Arcy, Ann. Missouri Bot. Gard. 65: 4. 1978. [1979]—FIG. 1.

Gerardia hispidula Mart., Nov. Gen. Sp. Pl. 3: 13. 1929. TYPE: not seen.
Anisantherina hispidula (Mart.) Pennell, Mem. Torrey Bot. Club 16: 106. 1920.

Erect, wiry annual *herbs* to 50 cm tall, often drying black; stems branching, slender, hispidulous with straight, multicellular hairs. *Leaves* opposite below, sometimes alternate above, to 8 cm long, linear, costate, the margins sparingly denticulate, scabrous above, glabrate beneath. *Inflorescences* open terminal racemes or panicles; pedicels 10–20 mm long, stiff, slender, glabrous, subtended by a leaf or bract, bearing two scalelike bracts about ½ way along the length. *Flowers* with the calyx campanulate cyathiform, ca. 6 mm long, the 5 deltoid teeth apically acuminate to subulate, glabrous, slightly accrescent in fruit; corolla pink, campanulate, 10–12 mm long, the limb ca. 6 mm long, the lobes ca. 3 mm long; stamens 4, the filaments inserted at the bottom of the limb (top of constriction in the tube), long pilose upwards, the anther thecae unequal, divergent, included. *Capsule* exserted 3–5 mm (¼ of the length), dehiscing septicidally

FIGURE 1. *Agalinis hispidula* (Mart.) D'Arcy.—A. Habit (×½).—B. Stamens. Note one reduced theca in each anther (×5½). [After *Allen* 821 (MO).]

and also sometimes loculicidally, the septum remaining with the capsule, the placenta dark, shiny, pitted.

This species may be recognized by its wiry, linear leaves and showy, bell-like pink flowers. In Panama it grows on open savannahs. *Agalinis hispidula* ranges from Guatemala to Brasil, occurring in similar open habitats. In Belize it occurs in pineland savannahs.

Because the anther thecae are slightly unequal, Pennell segregated this species as the genus *Anisantherina*. The Old World genus *Sopubia* is very much like *Gerardia* but is distinct in its singular anther thecae (Hansen, 1975). One cell of the anther is reduced to a fingerlike process which is directed downwards from the other. The reduction of anther cell in *Agalinis hispidula* is much less advanced and the shape of the two cells is similar. Pennell commented on possible affinity of this species with Old World stocks and drew attention to the condition in *Sopubia*, but he thought that *Agalinis hispidula* is more closely related to *Buchnera* and *Harveya* of the Old World than to other species of *Agalinis* in the Americas. His hypothesis does not evoke confidence.

COCLÉ: Natá, 50 m, *Allen 821* (MO, US). Hills W of Soná, *Allen 1070* (MO). Sabana de Dormisolo near Chepo, *Pittier 4664* (US). Aguadulce, *Pittier 4857* (US).

2. ALECTRA

Alectra[3] Thunberg, Nov. Gen. Pl. 81. 1784. TYPE: *A. capensis* Thunb.

Erect, wiry *herbs* parasitizing the roots of other plants. *Leaves* opposite or alternate, crenate to toothed, often scabrous, subsessile or petiolate, often appearing 3-nerved. *Inflorescences* solitary flowers in the upper leaf axils, sometimes appearing racemose; pedicels with a narrow bract near the apex. *Flowers* with the calyx campanulate, the 5 short lobes alike; corolla campanulate, variously exserted; stamens 4, the filaments glabrous or bearded, the anthers sometimes mucronate. ***Fruiting calyx*** sometimes accrescent.

Alectra is a primarily African genus with about 40 species in all. Two species occur in the New World. The plants are parasites on the roots of other plants but have normally developed leaves. The leaves may be opposite or alternate. Most collections dry without evident flowers, and the latest revision of the genus (Melchior, 1941) did not provide full descriptions of floral details, hence the brief description above.

Literature:

Melchior, H. 1941. Die Gattung *Alectra* Thunb., Notizbl. Bot. Gart. Berlin-Dahlem 15: 423–447.

1. **Alectra aspera** (Cham. & Schlecht.) L. O. Williams, Fieldiana, Bot. 34: 118. 1972.—FIG. 2.

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[3] For a list of synonyms see Melchior (1941). Only this name has been used for Central American material.

B
A

Pedicularis melampyroides L. Cl. Rich., Actes Soc. Hist. Nat. Paris 1: 111. 1792. TYPE: not seen.
Glossostylis aspera Cham. & Schlecht., Linnaea 3: 22. 1828. TYPE: Brazil, *Beyrich* (?MO).
Alectra brasiliensis Benth. in DC., Prodr. 10: 339. 1846. Authentic specimens: Brazil, *Gardner 567*, *Salzmann* (both MO).
Alectra melampyroides (L. Cl. Rich.) Kuntze, Rev. Gen. Pl. 2: 458. 1891, not *Alectra melampyroides* Benth. in DC., Prodr. 10: 339. 1846.
Melasma melampyroides (L. Cl. Rich.) Pennell in Britton & Wilson, Sci. Surv. P. R. & V. I. 6: 188. 1925.

Strict, erect *herbs* to 60 cm tall, stems wiry, hirsute with brownish, weak, several-celled hairs. *Leaves* opposite to alternate, subsessile, lanceolate, ovate or deltoid, apically acute, basally cuneate or truncate, the margins crenate to dentate, the teeth often salient, mostly 2–4 cm long, 8–16 cm wide, the midvein prominent on both sides and a pair of flanking longitudinal veins conspicuous beneath, the minor pinnate venation evident beneath, obscure above, scabrous above, scabridulous beneath with short, acicular hairs on multicellular bases, shiny above; petioles flat, broadly cuneate, 1–2 mm long. *Inflorescences* solitary flowers in the upper leaf axils, sometimes aggregated to appear racemose, the pedicels stout, glabrate, ca. 2 mm long, a linear to narrowly obovate hirsute bract arising from just below the apex. *Flowers* with the calyx broadly campanulate, hirsute, ca. 8 mm long, lobed about ⅓ way down, the lobes somewhat unequal, deltoid with subulate tips; corolla yellow, only slightly exserted, 1.0–1.3 cm long; stamens 4, didynamous, the anther theca forming an inverted U, 1.5 mm long over the filament apex; style circinnate in bud, 2-lobed. *Capsule* depressed globose, mostly included in the calyx which ruptures irregularly with age.

Although a number of collections were available from Central America, none had well preserved flowers, hence the omission of floral details above.

All Panamanian collections of *Alectra aspera* are from the Canal Zone and most are from the Pipeline Road just north of Gamboa, an area of slight disturbance in premontane wet forest. It grows in the open. The species ranges from Brazil to Guatemala and it occurs in the Antilles.

CANAL ZONE: En Gamboa en la Navy Pipeline, *Correa et al. 1704* (MO). Pipeline Road N of Gamboa Gate, *D'Arcy 9294* (MO); *Gentry 2652* (MO, PMA), *6675* (MO); *Maas & Dressler 714* (MO); *Nee 8431* (MO). Río Pedro Miguel near East Paraiso, *Standley 3004* (US). Pipeline Road N of Gamboa Gate, *Wilbur & Teeri 13411* (DUKE).

3. ANGELONIA

Angelonia Humboldt & Bonpland, Pl. Aequin. 2: 92. 1809. TYPE: *A. salicariaefolia* H. & B.

Erect or prostrate *herbs* or *shrubs*, pubescent with multicellular, often glandular hairs. *Leaves* subopposite, opposite below, mostly toothed, subentire, pinnately nerved, mostly without a defined petiole. *Inflorescences* solitary flowers

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FIGURE 2. *Alectra aspera* (Cham. & Schlecht.) L. O. Williams.—A. Habit (×1).—B. Flower bud showing stamens and style. Part of calyx removed (×4). [After *Wilbur & Teeri 13411* (DUKE).]

in the leaf axils but sometimes aggregated into showy racemes or spikes, the pedicels sometimes with minute basal bracts. *Flowers* strongly zygomorphic, the calyx 5-lobed to the base, the lobes ovate, alike, appearing imbricate; corolla cupular campanulate with 2 widely flaring lips, the upper lip 2-lobed, the lower lip 3-lobed with 2 pollen-collecting sacs, the lobes all similar; anthers 4, the filaments short, inserted near the base of the corolla tube, the anthers alike, the 2 thecae strongly divaricate and basally connate, situated at the throat against the upper side of the corolla; the stigma capitate, situated near the anthers. *Capsule* globose, dehiscing into 2 valves, the placentas honeycomblike.

Angelonia includes about 25 species in South America and two other species in Central America. The species treated here also occurs in the Antilles. At least two species are widely cultivated.

1. **Angelonia angustifolia** Benth. in DC., Prodr. 10: 254. 1846. TYPE: Mexico, not seen.

Erect perennial *herbs* to 60 cm tall, rarely scapose, the stems sparingly pilose with peak, multicellular gland-tipped hairs, drying sulcate. *Leaves* subopposite, oblanceolate, apically acuminate or acute, basally acute, minutely and distantly serrate in the distal half, the midvein prominent, the 2–3 lateral veins often indistinct, glabrous; petiole not defined, the leaf base concaulescent forming a pair of ridges on the stem. *Inflorescences* solitary flowers in the leaf axils, aggregated to form terminal racemes with reduced leaves; pedicels slender, 10–15 mm long, sparingly pilose, basally flanked by two minute, glabrous, acicular, scalelike bracts. *Flowers* showy, zygomorphic, the calyx 3–4 mm long, 5-lobed to the base, the lobes ovate, apically acuminate, glabrous; corolla blue or violet with a green throat, 15–20 mm long, 2-lipped, the lips wide spreading, the upper lip 2-lobed with a shallow sinus, the lower lip with 3 spatulate lobes 6–10 mm long, the lobes all subequal, punctate dorsally, punctate and puberulent inside, sometimes ciliolate, the tube campanulate, apically 2-saccate on the lower side and with a short appendage (staminode?); stamens 4, alike, the filaments inserted near the base of the tube, the anthers 2-locular with divaricate, basally connate thecas situated against the top of the tube, not exserted; ovary narrowly ellipsoidal, the style short, the stigma situated among the anthers. *Capsule* subglobose, half exserted from the persistent calyx lobes, 4–8 mm across, dehiscing to the base into 2 valves, the placentas becoming honeycomblike.

This species is recognizable with its narrow glabrous leaves, showy, unusual shaped flowers, and small, globose capsules. It ranges from Mexico to Panama and is most common along the Caribbean lowlands. In Panama, most collections are from Bocas del Toro. This species is also cultivated as an ornamental, and the collections cited from the Canal Zone are all cultivated plants. "Porto Bello" (Nicaragua); "Boca de la Vieja" (Guatemala); "Angelon" (Colombia).

BOCAS DEL TORO: Almirante, *Blum 1369* (MO). Isla Colón, *Wedel 62* (MO). Old Bank Island, *Wedel 1961* (MO, US). Careening Cay, *Wedel 2811* (MO, NY, US). Bastimientos, *Wedel 2914* (MO, NY). COCLÉ: Natá, *Allen 821* (MO, NY, US). Boca del Toabré at confluence of Río Coclé del Norte, *Lewis et al. 5572* (DS, MO). Aguadulce, *Pittier 4857* (US). PANAMÁ: Cultivated, Cañasas, 100 m, *Duke 145002* (MO). Without other locality, *Heriberto*

294 (US). Garden in Panama City, *Maurice 755* (US). Sabana de Dormisolo near Chepo, *Pittier 4664* (US). Juan Díaz, *Standley 30525* (US).

4. BACOPA

Bacopa Aubl., Hist. Pl. Guiane 128, *tab. 48*. 1775. nomen cons. TYPE: *B. aquatica* Aubl.

Moniera Juss. ex P. Br., Civ. Nat. Hist. Jam. 269. 1756. nomen rejic. TYPE: *Gratiola monnieria* L. = *Bacopa monnieri* (L.) Pennell.

Monniera, mult. auct., orth. mut.

Brami Adans., Fam. Pl. 2: 208. 1763. nomen rejic. TYPE: Based on *Brami*, Rheede, Hort. Malabar. 10: 27, *tab. 14*. 1689.

Bramia Lam., Encycl. Méth. Bot. 1: 459. 1785. TYPE: *B. indica* Lam. = *Bacopa monnieri* (L.) Pennell.

Mella Vandelli, Fl. Lusit. Bras. Sp. 43. 1788. TYPE: Pub. without species.

Septas Loureiro, Fl. Cochinch. 392. 1790. non *Septas* L. 1760 (Crassulaceae). TYPE: *S. repens* Lour. = *Bacopa monnieri* (L.) Pennell.

Calytriplex Ruiz & Pavón, Fl. Peruv. Chil. Prodr. 96. 1794. TYPE: *C. obovata* R. & P.

Herpestis C. F. Gaertner, Fruct. Sem. Pl. 3: 186. 1807. TYPE: *H. rotundifolia* C. F. Gaertner = *Bacopa innominaia* (Maza) Alain.

Herpestes Kunth, Syn. Pl. 2: 124. 1823. = *Herpestis* Gaertn. orth. mut.

Habershamia Raf., Neogenyton 2. 1825. LECTOTYPE: *Monniera cuneifolia* (Michx.) Raf. = *Bacopa monnieri* (L.) Pennell.

Hydranthelium H.B.K., Nov. Gen. Sp. 7. ed. fol. 156. 1825. TYPE: *H. callitrichoides* H.B.K.

Macuillamia Raf., Neogenyton 2. 1825. TYPE: *M. rotundifolia* (Michx.) Raf. = *Bacopa rotundifolia* (Michx.) Wettst.

Geochorda Cham. & Schlecht., Linnaea 3: 11. 1828. TYPE: *G. cuneata* Cham. & Schlecht.

Caconapea Cham., Linnaea 8: 28. 1833. TYPE: *C. gratioles* Cham.

Ranaria Cham., Linnaea 8: 30. 1833. TYPE: *R. monnierioides* Cham. = *Bacopa monnierioides* (Cham.) Robinson.

Septilia Raf., Fl. Tell. 4: 68. 1836. TYPE: *S. repens* Raf. = *Bacopa monnieri* (L.) Pennell.

Amphianthus Torr., Ann. Lyceum Nat. Hist. New York 4: 82. 1837. TYPE: *A. pusillus* Torr.

Heinzelmannia Neck. ex Endl., Genera Pl. 682. 1839. nomen nudum in syn.

Hydrotrida Willd. ex Steud., Nom. Bot. ed. 2. 1: 783. 1840. nomen nudum. TYPE: *H. beccabunga* Steud.

Heptas Meisn., Pl. Vasc. Gen. 293. 1842–43? TYPE: *H. repens* Meisn. = *Bacopa monnieri* (L.) Pennell.

Ildefonsia Gardner, London J. Bot. 1: 184. 1842. non Schott ex Steudel, Nom. Bot. 427. 1821. nomen nudum. TYPE: *I. bibracteata* Gardner.

Anisocalyx Hance ex Walp., Ann. Bot. Syst. 3: 195. 1853. TYPE: *A. limanthiflorus* Hance = *Bacopa monnieri* (L.) Pennell.

Cardiolophus Griff., Not. Pl. Asiat. 4: 105. 1854. TYPE: *C. decussata* Griff.

Ranapalus Kellogg, Proc. Calif. Acad. Sci. 7: 113. 1877. TYPE: *R. eisenii* Kellogg = *Bacopa eisenii* (Kellogg) Pennell.

Hydrotrida Small, Fl. Miami 165. 1913. LECTOTYPE: *H. caroliniana* (Walt.) Small = *Bacopa caroliniana* (Walt.) Robinson.

Monocardia Pennell, Proc. Acad. Nat. Sci. Philadelphia 72: 155. 1920. TYPE: *M. violacea* Pennell = *Bacopa salzmannii* (Benth.) Edwall.

Herbs, often paludal, erect or sprawling, often glandular punctate. *Leaves* opposite, entire or rarely dissected, pinnately or digitately veined, often sessile and somewhat clasping. *Inflorescences* paniculate or solitary flowers in the axils, sometimes geminate, the pedicels sometimes bracteate. *Flowers* with the calyx 5-lobed to the base, the outer 3 larger and enclosing the inner 2; corolla 2-lipped, the upper lip entire or 2-lobed, the lower lip 2-lobed, sometimes pubescent; stamens 4, didynamous, inserted in the upper ½ of the tube, the anthers mostly alike, the thecae separate but proximal; ovary 2-carpellate, the ovules numerous, the style mostly straight, the stigma minutely 2-lobed. *Capsule* conical or obtuse,

apically dehiscent into 4 valves, the placenta persistent; seeds oblong, longitudinally reticulate.

This genus is defined by the unequal sepals, the outer three larger and enclosing the narrower inner two. Stamens are usually 4 but may be 2 in some species or even in some plants with usually 4 stamens. The leaves are mostly glabrate and often glandular punctate; stems are glabrate or pilose. The genus is found in a number of habitats but many species are paludal or aquatic. A few species are tolerant of brackish waters. Species range from southern Canada to warm temperate South America and in the Old World.

a. Flowers sessile, fruiting pedicels less than 2 mm long; leaves 1 costate or pinnately veined. Plants erect.
  b. Stems pilose; fruiting calyces more than 3 mm long ---------- 1. *B. axillaris*
  bb. Stems puberulent or glabrate; fruiting calyces less than 3 mm long.
    c. Capsules copiously glandular, long; stems glabrous, sparingly glandular; leaves basally narrowed and often appearing petiolate ---------- 8. *B. sessiliflora*
    cc. Capsules eglandular; stems pubescent with whitish hairs; leaves basally broad and somewhat clasping ---------- 5. *B. monnierioides*
aa. Flowers conspicuously pedunculate, fruiting pedicels more than 3 mm long, mostly longer than the leaves; leaves palmately nerved or 1 costate; plants erect, creeping or floating.
  d. Outer fruiting sepals basally cordate, covering the capsule.
    e. Fruiting sepals about as long as the pedicels, puberulent; stems puberulent ---------- 2. *B. bacopoides*
    ee. Fruiting sepals much shorter than the peduncles, long ciliate; stems pilose ---------- 7. *B. salzmannii*
  dd. Outer fruiting sepals basally narrowed, mostly not completely covering the capsule.
    f. Leaves basally auriculate or hastate; leaves apically obtuse or acute; plants erect ---------- 3. *B. laxiflora*
    ff. Leaves basally narrowed; apically bluntly obtuse or rounded; plants creeping or floating.
      g. Leaves narrowly obovate or oblong, 1-nerved, less than 4 mm wide ---------- 4. *B. monnieri*
      gg. Leaves rotund, sometimes broadly obovate, conspicuously palmately many nerved, mostly more than 5 mm wide ---------- 6. *B. repens*

1. **Bacopa axillaris** (Benth.) Standl., J. Wash. Acad. Sci. 15: 460. 1925.

Herpestis axillaris Benth. in DC., Prodr. 10: 396. 1846. TYPE: Colombia, *Purdie* (K, not seen).
Caconapea axillaris (Benth.) Pennell, Proc. Acad. Nat. Sci. Philadelphia 72: 152. 1920.
Monniera axillaris (Benth.) Kuntze, Rev. Gen. Pl. 463. 1891.

Erect, sometimes branched *herbs*, the stems stout, soft, villous with stout, white, weak, uniseriate hairs mostly ca. 0.5 mm long, also with inconspicuous white, sessile glands; roots stout and fibrous. *Leaves* opposite, oblong or oblanceolate, apically acute, bluntly serrate in the upper ½, basally acuminate or cuneate to the slightly clasping insertion; to 5 cm long, 10 mm wide, the midvein prominent, the minor veins 3–5 on each side, obscure, strongly ascending, somewhat discolorous, dark green and inconspicuously punctate above, pale beneath and conspicuously glandular punctate with brown sessile discoid glands, usually glabrous on both sides except sometimes on the costa beneath. *Inflorescences* geminate fascicles of 3–6 flowers in the leaf axils; pedicels 1–2 mm long, glabrous, sometimes with a few sessile glands, conspicuously broadening upwards;

bracts 2, scalelike, narrowly ovate, 0.5 mm long at the pedicel apex. *Flowers* with the sepals distinct, the outer 3 broadly ovate, ca. 3 mm long, 2 mm wide, apically rounded or emarginate, entire or denticulate, the teeth sometimes with short, stout-based white hairs, otherwise glabrous, mostly with a few scattered white or brown sessile glands, palmately 5-nerved, the inner 2 sepals narrow, acute, prominently costate and reticulate, punctate with white and brown sessile glands, slightly shorter than the outer bracts; corolla white, ca. 3 mm long, slightly exserted from the calyx, tubular, contracted towards the middle, glabrous outside, pubescent at the contracted level inside, 4-lobed, the lobes short; stamens 4, the filaments glabrous, ca. 0.75 mm long, inserted at about the same level in the upper ½ of the tube, the anthers yellow, 0.5 mm long, the thecae separate; style 1.5 mm long, terete, the stigma horseshoe shaped, erose, peltate on the style. *Capsule* narrowly conical, 3 mm long, 4-valved, the valves 3-nerved; placentas flat, obtuse; seeds with a brownish, longitudinal reticulum, faboid rectangular, 0.5 mm long.

This species is distinguished by its villous stems and narrow, often discolorous leaves. The species occurs in swamps and other wet places in lowland central Panama. It is also reported from Colombia and Guatemala.

CANAL ZONE: Madden Dam, *Ebinger 864* (MO, US). Camino de la Granja, *Heriberto 159* (US). Cerro Gordo near Culebra, *Standley 26035* (PH, US). Old Las Cruces Trail between Fort Clayton and Corozal, *Standley 29055* (US). PANAMÁ: Sabanas N of Panama City, *Paul 559* (US). Las Sabanas, *Standley 25948* (PH, US). Near Juan Franco Race Track near Panama, *Standley 27829* (US). Near Matías Hernández, *Standley 28998* (US).

2. **Bacopa bacopoides** (Benth.) Pulle, Enum. Pl. Surinam. 415. 1906.

Herpestis bacopoides Benth. in DC., Prodr. 10: 399. 1846. TYPE: Brasil, *Gardner 1090* (MO).
B. bracteolata Pennell ex Standley, Contr. U.S. Natl. Herb. 27: 336. 1927. LECTOTYPE: Panama, *Pittier 6877* (US—"Caconapea bracteolata Pennell 1919") NY.

Herbs to 40 cm tall, branched, the stems drying angled, glabrate, apically with a few sessile globose tawny glands. *Leaves* opposite, ovate, obovate or broadly elliptical, ca. 2.5 mm long, 1.5–2.0 mm wide, apically obtuse, basally cuneate, the margins serrulate in the upper ⅔, glabrate, scabridulous above and along the midvein beneath, inconspicuously punctate with dark brown, subglobose glands, the midvein evident, with ca. 2 ascending veins on each side; petiole not defined. *Inflorescences* 1 or 2 flowers per leaf axil, sometimes paired, the pedicels slender, shorter than the leaves, about as long as the fruiting calyx, pilose with short white hairs or appearing pulverulent, angled, with a pair of small, cucullate, puberulent subopposite bracts near the top of the pedicel. *Flowers* with the calyx divided into 5 free sepals, the outer 3 sepals cordate, ca. 5 mm long, 4 mm wide, apically obtuse, puberulent, nervose, somewhat accrescent, the inner sepals narrow, acute, costate, ciliolate, shorter than the outer bracts; corolla white, 4–5 mm long; stamens 4, didynamous, the filaments 1.0–1.5 mm long, curved, inserted near the middle of the corolla tube, the anthers alike, ellipsoidal, the thecae 0.6 mm long, proximal, versatile, the connective short; ovary smooth, glabrous, sometimes glandular, the style distinct, terete, ca. 2 mm long, the stigmas bifurcate near the base, 0.7 mm long, the branches

terete. *Capsule* globose, sometimes apically glandular, the valves indurate, ca. 3 mm long, the outer sepals becoming winglike, to 15 mm long, coriaceous; seeds oblong, longitudinally reticulate, 0.5 mm long, tan or reddish brown.

This species may be recognized by its relatively large, cordate fruiting calyces which are often minutely puberulent. The leaves are sometimes basally contracted and thus petiolate.

Bacopa bacopoides occurs in Brasil, Surinam, Panama, Nicaragua, Guatemala and Belize. Some of the material treated by Williams (1973) as *B. lacertosa* Standley is actually this species. This species is quite similar to Philippine material going under the name *Herpestis floribunda* R. Br. In Panama *B. bacopoides* occurs in marshes and wet places at lower elevations.

CANAL ZONE: Navy Reservation N of Gamboa, *Dressler 3217* (MO, PMA). COCLÉ: Near Olá, *Pittier 5086* (US). COLÓN: 6 mi SW of Portobelo, *Luteyn 1421* (DUKE). LOS SANTOS: 3 mi W of Carreta, ca. 5 mi S of Las Tablas, *Burch et al. 1251* (MO). PANAMÁ: Agricultural Experiment Station at Matías Hernández, *Pittier 6877* (NY). Big swamp E of Río Tocumen, *Standley 2659* (US). Matías Hernández, *Standley 28999* (US—center specimen). Old Las Cruces Trail between Fort Clayton and Corozal, *Standley 29054* (PH, US), *29219* (US). Río Tocumen, *Standley 29425* (US). Between Matías Hernandez and Juan Díaz, *Standley 32012, 32085* (both US).

3. **Bacopa laxiflora** (Benth.) Edwall, Bol. Commiss. Geogr. Estado São Paulo 13: 180. 1897.

Herpestis laxiflora Benth. in DC., Prodr. 10: 396. 1846. TYPE: Brasil, *Gardner 2702* (?K, not seen).
Herpestis auriculata Robinson, Proc. Amer. Acad. Arts 26: 172. 1891. TYPE: Mexico, *Pringle 2937* (GH, not seen).
Bacopa auriculata (Rob.) Greenm., Publ. Field Mus. Nat. Hist., Bot. Ser. 2: 262. 1907.
Caconapea auriculata (Rob.) Pennell, Proc. Acad. Nat. Sci. Philadelphia 72: 150. 1920.
Mella laxiflora (Benth.) Pennell. Notul. Nat. Acad. Nat. Sci. Philadelphia 46: 1. 1940.

Erect *herbs* to 45 cm tall, stems drying angled, apically slender, glabrate, sometimes with a few short gland-tipped hairs near the apex, much branched; roots fibrous, sometimes rooting at the lower nodes, the stems basally stout. *Leaves* opposite, oblong or ovate, to ca. 30 mm long and 10 mm wide, apically acute, serrate in the upper ⅔, basally short auriculate, the auricles sometimes denticulate, clasping and appearing perfoliate, the midvein prominent, the lateral veins ca. 5 on each side, drying obscure above and scabridulous with minute acropetal trichomes, glabrate and lighter beneath; petiole wanting. *Inflorescences* numerous, solitary or paired in the leaf axils, the pedicels slender, scabridulous, mostly exceeding the leaves with a pair of linear or narrowly ovate scalelike bractlets to 1 mm long immediately below each flower, the subtending leaves sometimes reduced to small bracts. *Flowers* small, the calyx with the outer 3 sepals ovate, apically acute, basally narrowed, costate, ca. 4 mm long, 2.5 mm wide, apically scabridulous, sometimes mucronulate, the 2 inner bracts narrow, costate, hyaline, ciliolate, shorter than the outer bracts; corolla purplish, pubescent within below the filament insertion; stamens 4, didynamous, the filaments inserted in the upper ½ of the corolla tube, glabrous, ca. 2 mm long, the anthers ellipsoid, ca. 0.7 mm long, versatile, the ventral 2 reduced; ovary glabrous, ovoid, the style distinct, terete, ca. 2.5 mm long, the stigmas distinct, ca. 1 mm long, bifurcate

for ⅔ of the length, inserted in a short, annular disc. *Capsule* subglobose, 3–4 mm long, indurate, eglandular, the placenta cuneiform; seeds longitudinally reticulate, reddish brown, 0.5 mm long.

Bacopa laxiflora is an erect herb, the leaves and flowers mostly numerous, but the leaves are often reduced and the hastate or auriculate nature of the leaf bases is not always conspicuous. The species is reported from Panama and from Brasil and one may presume it occurs in other neotropical countries.

COCLÉ: Aguadulce, *Pittier 4907* (NY, US). PANAMÁ: Road between Panama and Chepo, *Dodge et al. 16676* (MO). Las Sabanas, *Heriberto 150* (US). 1 mi W of Juan Díaz, *Killip 3079* (US). Las Sabanas, *Standley 25945* (US). Near big swamp E of Río Tocumen, *Standley 26721* (PH, US). Near Matías Hernández, *Standley 28999* (MO—part, PH).

4. **Bacopa monnieri**[4] (L.) Pennell, Proc. Acad. Nat. Sci. Philadelphia 98: 98. 1946. Based on *Lysimachia monnieri* L.

Lysimachia monnieri L., Cent. 2. Pl. 9. 1756. TYPE: South America, *Hallman* (not seen).
Gratiola monnieria L., Amoen. Acad. 4: 306. 1759. TYPE: Jamaica, *P. Browne* (not seen).
Bacopa monnieria (L.) Edwall, Bol. Commiss. Geogr. Estad. São Paulo 13: 180. 1897. Based on *Gratiola monnieria* L.

Glabrous paludal *herbs*, the stems procumbent, mostly eglandular. *Leaves* opposite, somewhat succulent, narrowly obovate to spathulate, entire, apically rounded, basally cuneate, glandular punctate, the midvein apparent, palmately 3-nerved, the midvein evident but the 2–4 lateral veins obscure; petioles undifferentiated, the cuneate blades appearing slightly clasping perfoliate. *Inflorescence* a solitary flower in a leaf axil, the pedicels slender but broadening upwards, becoming 1–2 cm long in fruit, with 2 sepal-like, narrow, opposite apical bracts subtending the flower. *Flower* 7–9 mm long, the calyx imbricate, the 2 outer bracts equal, broadly ovate deltoid, 5 mm long, 2–3 mm wide, conspicuously 1-nerved, keeled, the 3 unequal inner sepals narrow, ranging from slightly shorter to slightly longer than the outer bracts; corolla tubular, ca. 8 mm long, glabrous, 5-lobed ¼–⅓ way down, the lobes subequal, white, pale purple or blue; stamens 4, the filaments glabrous, inserted unequally near the top of the tube, compressed, the anthers black, linear or curved, the thecae versatile, affixed near the middle, elongate, ca. 1.5 mm long and proximally connate for most of their length, little exserted; ovary narrowly oblong, ca. 4 mm long and 1 mm wide, the style discrete, ca. 4 mm long, terete, apically curved downwards, the stigma flat, slightly 2-lobed. *Capsule* loculicidal and septicidal to the base, the valves separating at the base, ca. 2 mm long, the placenta narrow, peglike, foveate, the septum translucent, hyaline, extending ca. 0.75 mm beyond the placenta on each side; seeds numerous, ca. 0.5 mm long, longitudinally reticulate, the reticulum reddish brown.

This is one of the most widespread species of *Bacopa*, and unlike some of the other species of *Bacopa* in Panama, it is usually found creeping in mud at the edges of standing water. It can tolerate somewhat brackish water and is often

[4] Many synonyms have been used for this species. Only the names given here relate directly to Panamanian plants.

found near the sea. The narrowly oblong or oblanceolate leaves and downward curving fruiting pedicels help to identify it.

BOCAS DEL TORO: Around air strip, *D'Arcy 11233* (MO). SW of Bocas at Maccaw Hills, Isla Colon, *Wedel 532* (MO). CANAL ZONE: Chagres, *Fendler 217* (MO). CHIRIQUÍ: El Pedregal de David, *Pittier 3377* (NY, US). COLÓN: Manzanillo Island, *Hayes 694* (NY). PANAMÁ: Panamá la Vieja, *Maurice 809* (US). SAN BLAS: Through cultivation on mainland in front of Ustupo, *D'Arcy 9514* (MO). Mulatuppa, *Duke 8504* (MO). Mainland near Isla Mosquito, *Duke 8880* (MO, OS). Mainland opposite Ailigandí, *Lewis et al. 214* (MO). Island village of Mamitupo, *Warner 212* (MO).

5. **Bacopa monnierioides** (Cham.) Robinson, Proc. Amer. Acad. Arts 44: 614. 1909.

Ranaria monnierioides Cham., Linnaea 8: 31. 1833. TYPE: Brasil, *Sello* (not seen).
Herpestis ranaria (Cham.) Benth., Hook. Companion Bot. Mag. 2: 57. 1836. Based on *Ranaria monnierioides* Cham.
Bacopa ranaria (Cham.) Chod. & Hassl., Bull. Herb. Boissier sér. 2, 4: 288. 1904.
Caconapea appressa Penn., Proc. Acad. Nat. Sci. Philadelphia 72: 152. 1920. TYPE: Colombia, *Pennell 1460* (MO, NY).
Bacopa parviflora Penn. ex Standley, Contr. U.S. Natl. Herb. 27: 336. 1928. LECTOTYPE: Panama, *Pittier 2462* (US).
Bacopa parviflora Standl. ex Williams, Fieldiana, Bot. 34: 118. 1972. TYPE: Panama, *Killip 3240* (F, not seen, MO). Redundant name.
Caconapea parviflora Pennell, ined. TYPE: Panama, *Pittier 2462* (US).

Erect *herbs* to 45 cm tall, sometimes rooting at the lower nodes; lower stems stout, soft, the upper stems slender, puberulent with weak, curled whitish hairs, drying angled; roots short and fibrous. *Leaves* opposite, narrowly oblong, to 3 cm long and 8 mm wide, apically obtuse or acute, basally clasping, not narrowed into a petiole, the margins entire or minutely denticulate, sometimes slightly inrolled, the midvein prominent, the lateral venation palmate, strongly ascending, obscure, glabrous, both sides punctate with numerous sessile annular glands. *Inflorescences* geminate fascicles of 1–5 flowers in the leaf axils, the subtending leaves sometimes reduced to small bracts; pedicels to 1 mm long, ebracteate, drying angled. *Flowers* minute, calyx ca. 1.5 mm long, lobed to the base, the outer lobes ovate, to 0.7 mm wide, prominently costate, conspicuously punctate with sessile, annular glands, the inner 2 lobes narrow, acute, minutely ciliate; corolla white or bluish white, tubular, 4-lobed, exserted ca. 0.5 mm from the calyx, white drying orange; stamens 4, the filaments glabrous, unequal, inserted high on the corolla tube, the anthers yellow, dorsifixed, the thecae proximal, the upper $\frac{1}{2}$ connate; ovary ellipsoid, reddish, smooth but sometimes drying longitudinally nervate, ca. 0.7 mm long, the style discrete, positioned on a minute pedicel, compressed, the stigma convolute, crestlike. *Capsule* ca. 1.5 mm long, splitting to the base, the valves indurate, eglandular; seeds numerous.

Bacopa monnierioides is similar to *B. sessiliflora* but has puberulent stems, especially on emerging, the locules of the anthers are divergent, and the capsule is eglandular or nearly so. The leaves subtending flowers (bracts) tend to remain basally broad even when much reduced, while in *B. sessiliflora* they tend to become narrow as well as smaller.

This species is widespread, ranging from Paraguay to Guatemala, and if *B.*

beccabunga (Griseb.) Pennell is considered synonymous, it also occurs in Cuba. In Panama it grows erect in swamps and wet savannahs.

CANAL ZONE: Beneath old Miraflores Bridge, *Dwyer 54* (MO). Old Las Cruces Trail between Fort Clayton and Corozal, *Standley 29223* (US). COLÓN: Forests around Portobelo, *Pittier 2462* (US). PANAMÁ: Savannahs near Chepo, *Duke 6035* (MO). Las Sabanas, *Heriberto 158* (US). Between the Tapia and Tocumen Rivers, *Killip 3240* (MO, US). Sabanas N of Panama City, *Paul 574* (US). Sabana de Juan Corso near Chepo, *Pittier 4676* (US). Las Sabanas, *Standley 25946* (PH, US). Near big swamp E of Río Tocumen, *Standley 26717* (PH, US). Juan Franco Race Track, *Standley 27828* (PH, US). Near Matías Hernández, *Standley 29002* (PH, US). Nuevo San Francisco, *Standley 30771* (US). Between Pacora and Chepo, *Woodson et al. 1649* (MO). SAN BLAS: Weeds of Mandinga Airport, *Duke 14826* (OS).

6. **Bacopa repens** (Sw.) Wettst. in Engl. & Prantl., Nat. Pflanzenfam. IV 3b: 76. 1895.

Gratiola repens Sw., Prodr. Veg. Ind. Occ. 14. 1788. TYPE: Jamaica, *Swartz* (not seen).
Herpestis repens (Sw.) Schlecht. & Cham., Linnaea 5: 107. 1830.
Macuillamia limosa Pennell, Proc. Acad. Nat. Sci. Philadelphia 72: 158. 1920. TYPE: Colombia, *Pennell 2927* (NY, US).
Bacopa limosa (Penn.) Standley, Contr. U.S. Natl. Herb. 27: 336. 1928.
Macuillamia repens (Sw.) Pennell, Acad. Nat. Sci. Philadelphia Monogr. 1: 60. 1935.

Aquatic or paludal *herbs*, stems stout but weak and prostrate, fistulose, drying flat, pubescent with spreading white hairs, glabrescent; roots fibrous, sometimes rooting at the nodes. *Leaves* obovate, elliptical or orbicular, apically obtuse or round, basally cuneate or slightly clasping, to 20 mm long, 15 mm wide, palmately many nerved, glabrous or pubescent, the margins entire or somewhat sinuate. *Inflorescences* 1(–3) flowers in the leaf axils, the peduncles slender, pilose, ca. 8 mm long, slightly longer in fruit, terete or drying angled, ebracteate. *Flowers* with 4–5 free sepals, the outer 2 sepals 2.5 mm long, 1.5 mm wide, entire, oblong, apically blunt acute, basally narrowed, nervose, glabrate or pilose, sometimes ciliate, the inner 2 sepals narrower, thin costate, ciliolate, shorter than the outer sepals; corolla white, the throat ?yellow, 3 mm long; stamens 4, the filaments glabrous, inserted at the top of the corolla tube, the anthers dark, broadly ellipsoidal, ca. 0.7 mm long, the thecae proximal; ovary glabrous, the style apically furcate, the stigmas 2-lobed, peltate, the style basally tapering gradually into the ovary, the style 1 mm long. *Capsule* globose, ca. 2 mm long, partly enclosed by the accrescent sepals, the sepals becoming 3–4 mm long.

This species may be recognized by its glabrescent stems, rotund leaves and small flowers and fruits. The only other Panamanian species of *Bacopa* with rotund leaves, *B. salzmannii*, has conspicuously pilose stems and much larger fruits.

Bacopa repens is found in swamps and other wet places in lowland Panama. It ranges from southern Mexico into South America and the Antilles. It closely resembles *B. rotundifolia* (Michx.) Wettst. which has slightly larger flowers, pedicels, and capsules, and sepals shaped slightly differently. *Bacopa rotundifolia* is a species of the southeastern United States.

COCLÉ: Between Las Margaritas and El Valle, *Woodson et al. 1754* (MO). DARIÉN: El Real, Río Tuira, *Stern et al. 451* (MO, US). Edge of road on Othon's farm, El Real, *Stern*

et al. 810 (MO, US). PANAMÁ: 5–6 mi E of Chepo on Panamerican Highway, *Duke 4019* (MO). Las Sabanas in swamp, *Heriberto 148* (US).

7. **Bacopa salzmannii** (Benth.) Edwall, Bol. Commiss. Geogr. Estado São Paulo 13: 176, 181. 1897.—FIG. 3.

Herpestis salzmannii Benth. in Hook., Companion Bot. Mag. 2: 58. 1836. TYPE: Brazil, *Salzmann 400* (MO).

Bacopa salzmannii (Benth.) Chod. & Hassl., Bull. Herb. Boissier sér. 2. 4: 290. 1904. Redundant combination.

Monocardia humilis Pennell, Proc. Acad. Nat. Sci. Philadelphia 72: 157. 1920. TYPE: Colombia, *Rusby & Pennell 1065* (NY, US).

?*M. lilacina* Pennell, Proc. Acad. Nat. Sci. Philadelphia 72: 156. 1920. TYPE: Colombia, *Pennell 1476* (NY, US).

M. violacea Pennell, Proc. Acad. Nat. Sci. Philadelphia 72: 156. 1920. TYPE: Colombia, *Pennell 1480* (NY, US).

Bacopa humilis (Pennell) Standley, J. Wash. Acad. Sci. 15: 460. 1925.

B. violacea (Pennell) Standley, J. Wash. Acad. Sci. 15: 460. 1925.

Herpestis ciliata Pennell, Notul. Nat. Acad. Nat. Sci. Philadelphia 46: 2. 1940. TYPE: Guyana, *Smith 2281* (NY).

Aquatic *herbs*, floating or prostrate on mud, sometimes ascending, sparingly branched, the stems stout, soft, hirsute with slender, sturdy uniseriate hairs, the basal cell enlarged, and with scattered globose sessile glands, sometimes rooting at the nodes, the roots fibrous. *Leaves* opposite, often subtended by tufts of white hairs, rotund or broadly ovate, apically obtuse or round, to 1.5 cm long and 1.2 cm wide but often much smaller, basally truncate or subcordate with auricles clasping the stem, the margins entire, often ciliate, the surfaces glabrous or with long hairs, palmately many nerved; petioles obsolete, punctate with brownish orange glands. *Inflorescences* of solitary flowers in the axils of the leaves, often geminate, the pedicels slender, hirsute, exceeding the leaves; ebracteate. *Flowers* with the sepals free to the base, the outer 3 broad, ca. 6 mm long and 5 mm wide, apically obtuse or emarginate, basally truncate or subcordate, the costa and the margins ciliate, many nerved, the inner 2 sepals narrowly deltoid, costate, glandular, slightly shorter than the outer sepals, hirsute outside, glabrous within; corolla blue or white, slightly exserted, ca. 7 mm long, 4-lobed, the upper lobe emarginate; stamens 4, the filaments glabrous, ca. 1 mm long, inserted near the top of the tube, the anthers linear, ca. 1.5 mm long, the thecae versatile, medifixed, connate along ½, free but proximal along the other ½; the ovary narrow, 1 mm long, glabrous, sulcate, the style terete, distinct, 3 mm long, apically curved, the stigma capitate, convoluted and slightly 2-lobed. *Capsule* ca. 3 mm long; seeds numerous, oblong, ca. 0.5 mm long, longitudinally reticulate, reddish brown.

Bacopa salzmannii may be recognized by its stout pilose stems and rotund leaves. It is generally prostrate.

The species occurs in lowland Panama in bogs, marshes, and other wet places. It ranges from southern Mexico to Brasil and it occurs in the Antilles.

BOCAS DEL TORO: Chiriquicito to 5 mi S along Río Guarumo, *Lewis et al. 2008* (MO, US). CANAL ZONE: Chagres, *Fendler 212* (MO). Gatún Lake, *Seibert 636* (MO, PH). Barro Colorado Island, *Shattuck* 15 July 1934 (MO). Juan Franco Race Track near Panama, *Standley 27827* (US). Old Las Cruces Trail between Fort Clayton and Corozal, *Standley*

FIGURE 3. *Bacopa salzmannii* (Benth.) Edwall.—A. Habit (×7/10).—B. Fruiting calyx (×4⅕). [After *Seibert 636* (MO).]

29218 (PH, US). Río Pedro Miguel near East Paraiso, *Standley 30044* (MO). CHIRIQUÍ: Marsh ca. 12 km W of El Hato, *D'Arcy 10882* (MO). Boqueté, 3800 ft, *Davidson 573* (MO, US). Francés Arriba School ca. 14 mi N of David, 1200 ft, *Lewis et al. 659* (MO, US). Marsh 1.6 mi NW of El Hato del Volcán towards Costa Rica border, *Luteyn 820* (DUKE). Las Lagunas W of El Hato del Volcán, 1400 m, *Wilbur et al. 10992* (DUKE). Boqueté, 1200–1500 m, *Woodson & Schery 707* (MO). Finca Lérida to Boquete, 1300–1500 m, *Woodson et al. 1150* (MO, NY). COCLÉ: El Valle de Antón, 600 m, *Allen 1996* (MO, NY, US). La Yeguada, 500–1000 m, *D'Arcy 11285* (MO). Km 21 on road to El Valle, *Gentry 5618* (MO). El Valle de Antón, 1000–2000 ft, *Lewis et al. 2504, 2572* (both DS, MO). Boca del Toabré at confluence of Río Coclé del Norte, *Lewis et al. 5553* (DS, MO). El Valle de Antón 500–700 m, *Seibert 487* (MO, NY, PH). La Mesa 3 km N of El Valle, 850 m, *Wilbur et al. 15627* (DUKE). Penonomé, *Williams 199* (NY, US). Between Las Margaritas and El Valle, *Woodson et al. 1721* (MO, PH, NY). COLÓN: Miguel de la Borda, *Croat 10070* (MO). Around Portobelo, 5–100 m, *Pittier 2456* (NY, US). PANAMÁ: Road between Panamá and Chepo, *Dodge et al. 16678* (MO). Las Sabanas, *Heriberto 148* (US); *Paul 567* (US). Laguna de Portala near Chepo, *Pittier 4608* (US). Las Sabanas, *Standley 25947* (US). Big swamp E of Río Tocumen, *Standley 26540* (US), *26661* (PH, US). Near Matías Hernández, *Standley 29001* (PH, US). VERAGUAS: Hills W of Soná, *Allen 1067* (MO, PH, US).

8. **Bacopa sessiliflora** (Benth.) Pulle, Enum. Pl. Surinam 415. 1906.

Herpestis sessiliflora Benth., Companion Bot. Mag. 2: 58. 1836. TYPE: Guyana, *Leprieur* (K, not seen).

Bacopa sessiliflora (Benth.) Edwall, Bol. Commiss. Geogr. Estado São Paulo 13: 176, 181. 1897. incomplete combination.

Caconapea conferta Pennell, Proc. Acad. Nat. Sci. Philadelphia 72: 153. 1920. TYPE: Colombia, *Pennell 1435* (MO, NY).

C. sessiliflora (Benth.) Pennell, Proc. Acad. Nat. Sci. Philadelphia 75: 11. 1923.

Erect *herbs* to 45 cm tall, glabrous, the stems mostly terete; roots fibrous. *Leaves* opposite, oblanceolate, mostly ca. 3 cm long, 4 mm wide, apically acute, the base narrowed but without a distinct petiole, serrate in the upper ½, copiously but inconspicuously punctate with brownish, annular glands on each side. *Inflorescences* solitary or fasciculate flowers in the leaf axils; pedicels glabrous, eglandular, to 1 mm long or obsolete, drying angled, bracts narrowly deltoid or linear, 1.0–1.5 mm long, costate, thin, located at the top of the pedicel. *Flowers* small, the calyx 5-lobed to the base, the outer 3 sepals 2–3 mm long, entire, apically obtuse, costate and nervose, with copious, globose, shiny tawny glands, the 2 inner sepals narrow, slightly shorter than the outer sepals, costate, sparingly glandular; corolla blue or white, ca. 4 mm long, exserted ca. 1 mm from the calyx, 5-lobed, compressed and somewhat 2-lipped, the lobes rotund, 0.5 mm long, the tube pilose within in the lower ½; stamens 4, the filaments terete, curved, inserted about the middle of the corolla tube, the anthers yellow, rotund, the thecae connate, dorsifixed, versatile; ovary ca. 1.25 mm long, densely glandular, the style ca. 1 mm long, mostly eglandular, distinct from the ovary, stigma slightly 2-lobed. *Capsule* 2–3 mm long, indurate, glandular, at least near the base and the apex, splitting apically, the placenta yellow, cuneiform; seeds numerous, ca. 0.25 mm long, dark brown, reticulate.

Bacopa sessiliflora is similar to *B. monnierioides* which also has nearly sessile small flowers and narrow leaves, but it has conspicuously glandular capsules and somewhat different leaves. The leaves of *B. monnierioides* have a greater tendency

to clasp the stem and thus have less contracted petiolar regions, and the leaves of *B. monnierioides* are usually entire while those of *B. sessiliflora* are usually serrate.

Bacopa sessiliflora is found in wet marshes and other wet places in Panama. It has some tolerance for brackish water and is found behind beaches. The species ranges from Guatemala to Colombia and Surinam.

CANAL ZONE: Just E of Gatún Lock, *Duke 4309* (MO). Chagres, *Fendler 211* (MO, US). Cerro Gorda near Culebra, *Standley 26036* (US). Juan Franco Race Track near Panama, *Standley 37830* (PH, US). Old Las Cruces Trail between Fort Clayton and Corozal, *Standley 29217* (PH, US). Summit, *Standley 30055* (US). COCLÉ: Aguadulce, *Pittier 4897* (NY, US). COLÓN: Miguel de la Borda, *Croat 10069* (MO). Mouth of Río Piedras, *Lewis et al. 3188* (DS). LOS SANTOS: Monagre Beach 5 mi SE of Chitre, *Tyson et al. 3051* (MO). PANAMÁ: Las Sabanas, *Standley 25949* (US). Río Tapia, *Standley 28223* (US). Nuevo San Francisco, *Standley 30769* (US). Between Matias Hernández and Juan Diaz, *Standley 32024* (PH, US). Near Las Sabanas, *Standley 40773* (US).

5. BENJAMINIA

Benjaminia Mart., Fl. Bras. 10: 255. 1 June 1847. TYPE: *B. utricullariaeformis* Benj. ex Mart. = *B. reflexa* (Benth.) D'Arcy.

Quinquelobus Benj., Linnaea 20: 316; (before 1 June) 1847; Berichtigung 1. (1 August 1847). nomen nudum. LECTOTYPE: *Q. utricullariaeoides* Benj. = *Benjaminia reflexa* (Benth.) D'Arcy.

Naiadothrix Pennell, Mem. Torrey Bot. Club 16: 105. 1920. TYPE: *N. longipes* Pennell = *Benjaminia reflexa* (Benth.) D'Arcy.

Bacopa sect. *Chaetodiscus* subsect. *Naiadothrix* Pennell, Proc. Acad. Nat. Sci. Philadelphia 98: 98. 1946.

Submerged aquatic *herbs*, sometimes rooting at the nodes, glabrate or pubescent, glandular punctate. *Leaves* verticillate, pinnately dissected, flat, the segments filiform. *Inflorescences* solitary flowers in the leaf axils, the pedicels elongating in fruit, ebracteate. *Flowers* with the calyx divided to near the base into 5 subequal narrow lobes; corolla 2-lipped, the lobes rounded; stamens 4, didynamous, the anthers equal, the thecae equal and proximal; ovary obtuse, 2-locular, the stigma flat and curved. *Capsule* ovoid, membranaceous, the seeds oblong, longitudinally reticulate, numerous.

This genus has long been considered congeneric with *Bacopa* but it differs notably in its dissected leaves and 5 subequal calyx lobes which are connate to slightly higher above the base. The pedicels lack bracts and the ovary is surrounded by sterile filaments or tufts, features present in some species of *Bacopa* but not in others. *Benjaminia* has also been considered closely allied to *Conobea* Aublet, but in that genus the leaves are serrate, not dissected, the calyx lobes are of 2 different sizes and the pedicels are apically bibracteolate. *Leucospora* Nutt. a monotypic genus of eastern North America, agrees superficially with *Benjaminia* in many details including the form of the leaves, flowers and fruit and in the pedicels lacking bracts, but the sepals are more deeply divided, there are no filaments around the ovary, and the lower anthers are separated on minute arms. In its leaf morphology *Benjaminia* is quite similar to the Asiatic *Limnophila* R. Br., but species of that genus always bear some entire or serrate leaves near

the inflorescence, quite different from the submerged, dissected leaves. *Benjaminia* is apparently monotypic, although a case can be made for separating plants from Belize from the type species. It is restricted to the neotropics.

The contorted formalities of nomenclature and status of *Benjaminia* and its type species were reviewed by Smith & Pires (1956). Benjamin first noted the genus in Linnaea 20: 316, listing *Quinquelobus* with four species, but because no generic description was provided, none of these names is validly published. One of his species, *Q. utricullariaeoides*, was without description but referred to his unpublished treatment in Martius' Flora Brasiliensis. Soon after, the Flora Brasiliensis treatment appeared, and Martius had altered the Lentibulariaceae manuscript of Benjamin, substituting the name *Benjaminia* for *Quinquelobus* and altering the name of the single species appearing therein from *utricullariaeoides* to *utricullariformis*. The type, *Gardner 4347*, was indicated. The date given in the front of the volume for the Lentibulariaceae is 1 June 1847. In corrections page (*Berichtigung*) dated 1 August 1847 appearing at the end of Linnaea vol. 20, Benjamin made transfers of his names in *Quinquelobus* into *Benjaminia*. He stated that the Flora Brasiliensis treatment had appeared after his paper listing *Quinquelobus* and referred to the whole sequence as an error on his part.

A year earlier, Bentham had published *Herpestis reflexa* based on the same collection, *Gardner 4347*. Bentham (1848) later noted that *Benjaminia utricularioides* (sic.) and his own *Herpestis reflexa* were based on the same type and belonged to the Scrophulariaceae and not to the Lentibulariaceae where Benjamin had placed his species. Benjamin (1849) protested Bentham's statements arguing that the material before him was indeed lentibulariaceous, suggesting that Bentham may have been working with different plants. In his Genera Plantarum, Bentham (1873) noted Benjamin's rejoiner but did not accept it, and he regarded *Quinquelobus* and *Benjaminia* as spurious. The figure presented by Benjamin in the Flora Brasiliensis agrees with the scrophulariaceous collection of *Gardner 4347* at MO in all respects, and his diagnosis notes "semina plurima minima elliptica," so it is assumed that Benjamin erred and that his plant was the same as the other parts of the collection at MO and K.

Literature:

Smith, L. B. & J. M. Pires. 1956. An evaluation of *Benjaminia* Martius ex Benjamin. J. Wash. Acad. Sci. 46: 86.

Benjaminia reflexa (Benth.) D'Arcy, comb. nov.—FIG. 4.

Herpestis reflexa Benth. in DC., Prodr. 10: 399. 1846. LECTOTYPE: Brasil, *Gardner 4347* (dupla MO).

Benjaminia utricullariaeformis Mart., Fl. Bras. 10: 256. 1847. TYPE: Brasil, Goyas, *Gardner 4347* (B, not seen; isotype MO).

Quinquelobus utricullariaeoides Benj., Linnaea 20: 316. 1847. = *Benjaminia utricullariformis* Benj. orth. mut. cf. Benjamin, Linnaea 20: Bericht. 1. 1847.

Monniera reflexa (Benth.) Kuntze, Rev. Gen. Pl. 2: 463. 1891.

Bacopa reflexa (Benth.) Edwall, Bol. Commiss. Geogr. Estado São Paulo 13: 176. 1897.

Naiadothrix longipes Pennell, Mem. Torrey Bot. Club 16: 105. 1920.

FIGURE 4. *Benjaminia reflexa* (Benth.) D'Arcy. Habit (×1). [After *Hunter & Steyermark 16718* (NY).]

N. reflexa (Benth.) Pennell, Mem. Torrey Bot. Club 16: 106. 1920.
Bacopa longipes (Pennell) Standley, Field Mus. Nat. Hist., Bot. Ser. 11: 141. 1932.
B. naias, Standley, Field Mus. Nat. Hist., Bot. Ser. 11: 141. 1932. TYPE: Belize, *Schipp 610* (F, holotype, not seen; isotype MO).

Rooted, submerged aquatic *herbs*; stems often branching, sometimes ridged, the nodes sometimes slightly jointed, glabrate or pubescent with weak, white, several-celled hairs, glandular punctate. *Leaves* 6–8 verticellate, 2–35 mm long, imparipinnately dissected, the 5–20 segments on each side flat, filiform, 0.5–12.0 mm long; petiole wanting or short, the leaf bases sometimes united into a rudimentary column. *Inflorescence* of solitary flowers in the leaf axils, usually only 1 per node, pedicels 0.5–18.0 mm long, becoming 10–25 mm long and stouter in fruit, holding flower ?and fruit above the water surface, ebracteate. *Flowers* 2–5 mm long in bud, the calyx mostly 2–5 mm long, 5-lobed to near the base, the lobes narrow, costate and cucullate, apically ciliolate, punctate, becoming more strongly angled and longer in fruit; corolla bluish or mauve with a yellow eye, lined, exserted ca. 5 mm from the calyx, 2-lipped, the lobes rounded, ?entire; stamens 4, the anthers versatile, all alike, and the thecae all alike, the filament apically narrowed and the connective not evidently enlarged; style straight, the stigma flattened and curved. *Capsule* ovoid, ca. 2.5 mm long, slightly shorter than the calyx, the pericarp membranous, perhaps not regularly dehiscent, the style persistent; seeds numerous, 0.6 mm long, tan or yellowish, longitudinally reticulate.

This species is conspicuously distinct from all other Panamanian Scrophulariaceae in its finely dissected leaves which closely resemble those of *Cabomba* (Nymphaeaceae). In *Cabomba*, the leaves are doubly compound, the pinnate leaflets arising from stalked verticels while in *Benjaminia reflexa* the verticels are sessile on the stems or nearly so. *Benjaminia reflexa* is superficially similar to *Bacopa myriophylloides* (Benth.) Pennell of South America. In that species, the leaves are not pinnate but digitate, and features of the flower are quite different, notably lacking sterile tufts of filaments around the ovary.

Little material of *Benjaminia* has accumulated in herbaria and the above synonymy is proposed with hesitation. The plants from Belize are much more robust and have more distinctly angled stems than other material seen, and Panamanian plants are more pubescent than those from elsewhere. Capsules of Cuban plants are apically flat or emarginate while those from Brasil are subacute. The capsules of the Cuban plants are also glandular while on Brasilian plants the glands are not evident. In spite of this variation, it is here assumed that all material seen is of one species, wide-ranging geographically and differing greatly in age and perhaps growing conditions. Contrary to Pennell, none of the plants is glabrous. The above description was prepared from a range of material at hand and not from Panamanian specimens only.

PANAMÁ: Aquatic pool in savanna, road to Chepo, *Hunter & Steyermark 16715* (PH), *16718* (NY, PH). Laguna de Portala near Chepo, 50 m, *Pittier 4604* (US).

6. BUCHNERA

Buchnera L., Sp. Pl. 630. 1753; Gen. Pl., ed. 5. 278. 1754. TYPE: *B. americana* L.

Piripea Aubl., Hist. Pl. Guiane 2: 628. 1775. TYPE: *P. palustris* Aubl. = *Buchnera palustris* (Aubl.) Spreng.

Bonnetia Neck., Elem. Bot. 1: 368. 1790, non *Bonnetia* Schreb. (1789—Theaceae), nec

Bonnetia Mart. (1826—Theaceae). nomen illegit., cited *Piripea* Aubl. TYPE: not designated.
Buechnera auct. = *Buchnera* orth. mut.

Annual or perennial *herbs*, mostly drying black, perhaps parasitic; stems sparingly branched, mostly wiry, slightly compressed or terete, mostly pubescent, often strigose, the hairs often stout based. *Leaves* narrow, the basal leaves opposite, sometimes small and broad, the cauline leaves often alternate, entire or remotely denticulate, pointed at both ends, (1–)3–5-nerved; petiole mostly obsolete. *Inflorescences* terminal spikes, the flowers subsessile, subtended by scalelike foliaceous bracts and by 2 ovate, usually ciliate bracts, the outermost usually larger. *Flowers* with the calyx tubular, sometimes broader above, 5-lobate, the lobes equal or conspicuously unequal, the tube 10-nerved, enervate between or conspicuously nervate between the major nerves, slightly accrescent in fruit; corolla salverform, the tube exserted, glabrous or pubescent outside, the limb with 5 subequal rotund lobes, the throat densely tufted with stout, moniliform hairs, the tube mostly pubescent below and pubescent with simple or few celled hairs below the point of stamen insertion; stamens 4, inserted in the bottom ½ of the tube, didynamous, the anthers ovoid or ovate, pointed apically, versatile, situated about ⅔ way up the tube; ovary ovoid, glabrous, the style simple, the stigma a linear extension of the style, perhaps inconspicuously 2-lobed, included. *Capsule* enveloped by the indurate fruiting calyx, sometimes slightly exserted, splitting loculicidally to the base into 2 elliptical valves, the dissepiment remaining with the valves as broad median ridges, the placenta narrowly cylindrical; seeds numerous, oblong, slightly angled, longitudinally ridged.

Buchnera includes about 100 species, about 16 occurring in the New World and ranging from eastern Canada to Argentina. The genus is relatively uniform in general appearance, sparingly branched wiry herbs with small, salverform white, blue or purplish corollas. In some species variously colored corollas occur in the same population. The calyx is shaped much like that of *Escobedea* with which *Buchnera* is usually allied. Species of *Buchnera* occupy open habitats and are tolerant of paludal conditions as well as extreme drought. In Panama, species of *Buchnera* bloom on dry savannahs when no other plants are in flower.

Literature:

Philcox, D. 1965. Revision of the New World species of *Buchnera* L. (Scrophulariaceae). Kew Bull. 18: 275–315.

a. Calyx with the areas between the 10 principal nerves enervate; corolla mostly white, the lobes entire, glabrous; inflorescence mostly open ..... 1. *B. pusilla*
aa. Calyx with evident nerves between the 10 principal nerves and hence appearing many nerved; corolla mostly pink or purplish, the lobes often crenulate, sometimes ciliate; inflorescence mostly crowded.
b. Corolla tube externally glabrous; leaves linear, appearing 1-nerved, glabrous except at the ciliate base; bracts glabrous except for the ciliate margin; calyx glabrous, the lobes acuminate; annual plants ..... 3. *B. weberbaueri*
bb. Corolla tube externally pilose; leaves lanceolate or oblong, mostly evidently 3-nerved, pubescent overall; bracts dorsally pubescent, especially apically; calyx pubescent, at least on the nerves, the lobes short-deltoid; perennial plants ..... 2. *B. rosea*

1. **Buchnera pusilla** H.B.K., Nov. Gen. Sp. Pl. 2: 340. 1818. TYPE: Colombia, *Humboldt & Bonpland* (B, not seen, destroyed fide Philcox 1965; photo MO). —FIG. 5.

B. tinctoria Bertol., Fl. Guatimal. 26. 1840. TYPE: Guatemala, *Bertoloni* (?BOLO, not seen).
B. major Polak., Linnaea 41: 588. 1877. TYPE: Costa Rica, *Polakowsky 519*, not seen.
B. mexicana Hemsl., Biol. Centr. Amer. Bot. 2: 457. 1881. TYPE: Mexico, *Seemann 2095* (K).
B. mexicana var. *minor* Hemsl., Biol. Centr. Amer., Bot. 2: 457. 1881. TYPE: Mexico, *Seemann 1506* (K).
B. minor (Hemsl.) Riley, Kew Bull. 1923: 117. 1923.
B. elongata sensu auct., non Sw.
B. elongata pilosa Benth., Bot. Voy. Sulphur 144. 1845. nomen nudum. TYPE: Mexico, *Schlechtendal 113*, not seen.
B. lithospermifolia sensu auct., non H.B.K.
B. pilosa Benth., Bot. Voy. Sulphur 144. 1845. nomen nudum.

Slender annual *herbs*, sparingly branched, to 30 cm tall, the stems wiry, scabrid with white, stout based mostly ascending short hairs and also with finer hairs, mostly somewhat compressed, inconspicuously ridged. Basal *leaves* obovate, to 10 mm long, glabrate but ciliate on the margin and the costa, the cauline leaves narrowly oblanceolate or linear, to 3 mm wide and 40 mm long, entire or with a few ill-spaced salient teeth, scabrid with stout based short acicular whitish or dirty colored hairs, in age the stout bases remaining as callose punctations, 3-nerved but usually appearing 1-nerved, the petiole not differentiated. *Inflorescence* mostly open, a terminal spike to 15 cm long, the outermost bracts ovate, shorter than the calyx except those towards the base of the inflorescence, the inner bract narrower, shorter, both bracts ciliate and scabrid with short, firm, acicular hairs, these often stout based. *Flowers* mostly white, sometimes blue, pink or purple, the calyx 5–7 mm long, tubular, 10-ribbed, the ribs prominent and conspicuously scabrid, the intermediate areas with obscure venation, mostly glabrous, the 5 teeth often quite unequal, narrowly acuminate, mostly 1–2 mm long, somewhat outcurving; corolla salverform, to 8 mm long, the tube exserted, mostly glabrous outside, the limb 5-lobed, the lobes 2–5 mm long, entire, glabrous, but sometimes minutely papillose ventrally, the throat slightly elevated above the patent lobes, tufted with sturdy hairs, sparingly pilose within with long weak hairs; stamens 4, the filaments inserted about ½ way up the tube, subequal, the anthers narrowly ovoid or oblong, pointed apically, 2-locular, situated in the top ½ of the corolla tube; ovary glabrous, 2-locular, narrowly conical, the style straight, glabrous, the stigma elongate, slightly expanded, sometimes compressed. *Capsule* included in the indurated, slightly accrescent calyx, mostly exceeding the calyx tube but not the lobes, the valves elliptical; seeds ca. 1 mm long, yellowish, oblong, longitudinally ridged.

This species is distinguished from other Panamanian species of *Buchnera* by its roughly scabrid flowering calyces which lack venation between the 10 ribs.

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FIGURE 5. *Buchnera*.—A, B. *Buchnera pusilla* H.B.K.—A. Habit (×7/10).—B. Calyx and bracts, corolla removed (×3½). [After *Pittier 5069* (US).]—C. *Buchnera weberbaueri* Diels. Calyx and bracts, corolla removed (×3½). [After *Piper 5542* (US).]

A
C
B

In fruit, this species may develop nerves between the calyx ribs. The usually glabrous corolla and entire, eciliate corolla lobes are also distinctive. One collection, *Ebinger 1077*, from the Azuero Peninsula, has corolla tubes with a few hairs at the apex, a condition quite unusual in the species. This collection seems in no other way different from other collections from throughout the range.

Buchnera pusilla is sometimes difficult to separate from *B. longifolia* H.B.K. (*B. elongata* Sw.) from the Antilles. Philcox (1965) noted that Antillean collections tend to have less sturdy hairs on the calyces and these hairs usually lack expanded bases. Material examined in this study did not evoke confidence in the separation. Both *B. pusilla* and *B. longifolia* were published at the same time, so that if the two names do apply to the same species, *B. longifolia* becomes a synonym of *B. pusilla.*

Buchnera pusilla ranges from Mexico to Ecuador and Brasil, and if the synonymy of *B. longifolia* is accepted, in the Antilles and south to Argentina.

CANAL ZONE: Chiva-Chiva, *Killip 3133* (PH, US). Alhajuela, Chagres River, *Killip 3217* (US). Chiva-Chiva Trail, Red Tank to Pueblo Nuevo, *Piper 5745* (PH, US). Sosa Hill, Balboa, *Standley 25296* (PH, US). Old Las Cruces Trail between Fort Clayton and Corozal, *Standley 29035* (US). Cocoli Island, Miraflores Lake, *White 289* (MO). CHIRIQUÍ: Lava flow between El Hato and Bambito, *D'Arcy 1011* (MO). Ca. 3 km NE of El Hato del Volcan at base of Volcán de Chiriquí, 1–3 km E of highway, 1500–1800 m, *Davidse & D'Arcy 10381* (MO). Cerro Vaca, 900–1136 m, *Pittier* (US). COCLÉ: E of Río Teta and Interamerican Highway, *Blum 1878* (MO). Near Santa Clara Beach, *Croat 9605* (MO). Picacho de Olá, *Pittier 5069* (US—right hand plants only). Penonomé, 50–1000 ft, *Williams 184* (NY). COLÓN: Savannas along drowned Río Azote Caballo, 66–70 m, *Dodge et al. 16838* (MO). HERRERA: Ocú, *Ebinger 1077* (MO, US). PANAMÁ: Pacora, 35 m, *Allen 1001* (MO). Between Panama and Chepo, *Dodge et al. 16659* (MO). Near beach at Nueva Gorgona, *Duke 4542a* (MO). Toward top of Cerro Campana, *Duke 6010* (DS, MO). Savannas near Chepo, *Duke 6055* (MO). Between Río Pacora and Chepo, *Dwyer et al. 5104* (MO). South Beach, San Jose Island, *Erlanson 529* (US), *569* (NY, US). Air strip and East Harbor, San Jose Island, *Harlow 77* (US). Llanos de Panamá Vieja, *Heriberto 289* (US). Savannas near Chepo, *Hunter & Allen 33* (MO). East Bay, San Jose Island, *Johnston 180* (MO, US). Savannas, *McBride 2659* (US). 7 mi S of Campana, *McDaniel 8316* (DUKE, MO). Savannas N of Panama City, *Paul 391* (US). Laguna de Portala near Chepo, *Pittier 4597* (US). Chepo, 60 m, *Pittier* (US). Sosa Hill, *Standley 26409* (US). Big swamp E of Río Tocumen, *Standley 26616* (US). Toboga Island, *Standley 28024* (US). Río Tapia, *Standley 28189* (US). Between Las Sabanas and Mátias Hernández, *Standley 31852* (PH, US). VERAGUAS: Near La Mesa, *Tyson 6056* (MO).

2. **Buchnera rosea** H.B.K., Nov. Gen. Sp. Pl. 2: 342. 1818. TYPE: Colombia, *Humboldt & Bonpland* (P, not seen; photo, MO).

B. lithospermifolia sensu auct., non H.B.K.

Perennial wiry *herb* to 1 m tall, sparingly branched, the stems terete or somewhat compressed, sometimes drying somewhat angled or grooved, puberulent but seldom strigulose, the 2–3 celled hairs microscopically tuberulate, the bases sometimes expanded. *Leaves* lanceolate, to 6 cm long, 10 mm wide, acute at both ends, entire or remotely denticulate, prominently 3(–5) nerved, the veins elevated beneath, scabrous to glabrate, the leaves smaller upwards, becoming scalelike and apparently 1-nerved at the inflorescence, pubescent on both sides with acicular hairs, more so beneath, glabrescent beneath except on the costa, the petiole obsolete. *Inflorescence* an elongate terminal spike, the flowers mostly aggregated and sometimes congested near the apex, the lower portion of the

rachis with greatly reduced leaves (bracts), the flowers subtended by 2 small bracts, the outermost larger, conspicuously ciliate and dorsally appressed pubescent. *Flowers* mostly pink or purplish, the calyx tubular, 5–6 mm long, the 5 deltoid lobes subequal, the tube 10-nerved with evident intermediate longitudinal nerves and thus appearing many nerved, mostly pubescent all over with short hairs, the bases sometimes expanded and callose, but not greatly so; corolla salverform, 6–9 mm long, the tube overall pubescent outside with short, weak hairs; the limb 5-lobed, 6–7 mm across, the lobes entire or crenulate-erose margined, ?emarginate ciliate, the throat tufted with stout hairs; stamens inserted in the lower ½ of the tube, the 2 pairs at nearly the same level, 1 pair of the filaments twice as long as the other, the anthers ovate, apiculate, versatile, becoming quite flat, situated in the upper ½ of the tube; ovary glabrous, the style simple, the stigma an elongate continuation of the style, not or hardly exceeding the anthers. *Fruiting calyx* 5–7 mm long, 20–30 nerved or reticulate between the 10 ribs, indurate, apically strigose with short, subappressed stout based hairs, the capsule about as long as the calyx lobes; seeds yellowish, longitudinally ridged, oblong, ca. 0.5 mm long.

Buchnera rosea is distinguished from *B. pusilla* by its pubescent corolla tube and by the nervate areas between the calyx ribs. It is distinguished from *B. weberbaueri* by its usually 3–5 nerved and pubescent leaves. *Buchnera rosea* ranges from Peru to Panama. Panamanian collections are much less robust than those seen from South America.

CANAL ZONE: Ancón Hill, *Killip 12076* (PH, US); *Piper 5542, 5546, 5577* (all US); *Standley 26346* (US). PANAMÁ: Isla Taboga, *Allen 1281* (MO, PH, US). Hills NE of Hacienda La Joya, *Dodge et al. 16881* (MO). Taboga Island, *Killip 3171* (US); *Macbride 2819* (PH, US); *Miller 2032* (US); *Pittier 3594* (US); *Standley 28024* (US); *Woodson et al. 1466* (MO).

3. **Buchnera weberbaueri** Diels, Bot. Jahrb. Syst. 37: 430. 1906. HOLOTYPE: Peru, *Weberbauer 4595* (B, destroyed, not seen; photo MO); NEOTYPES: Panama, *Terry 1273* (F, not seen, MO).—FIG. 5.

B. leiantha Standley, Field Mus. Nat. Hist., Bot. Ser. 22: 105. 1940. TYPE: Panama, *Terry 1273* (F, holotype; isotype, MO).

Wiry *herb* to 60 cm tall, mostly unbranched; stems terete or somewhat compressed, scabrous with stout acicular white hairs and finer shorter hairs, glabrescent. *Leaves* linear, to 3 cm long, to ca. 2 mm wide but mostly narrower, 3-nerved on wider leaves, mostly seemingly 1-nerved, the nerves indurate callose, glabrous except ciliate near the base. *Inflorescences* elongate terminal spikes, only the apical 10–25 mm floriferous, the basal portion with scalelike bracts, the flowers congested, subtended by 2–3 ovate bracts slightly more than ½ as long as the calyx, the innermost bracts much smaller, glabrous except for the ciliate margins. *Flowers* lavender, the calyx narrowly funnelform, 7–10 mm long, many nerved, glabrous, the lobes equal, acuminate, ca. 2 mm long; corolla tube to ca. 10 mm long, glabrous outside, the lobes rotund, ca. 3 mm long, sometimes sparingly ciliate and crenulate, the throat bearded. *Capsule* ovoid, glabrous, 6–8 mm long, included in the indurate calyx.

Buchnera weberbaueri ranges from Peru to Trinidad and west to Panama and Belize. In Panama it occurs at middle elevations in Chiriqui as well as at lower elevations in Cocle Province. Philcox described this species as an annual, but in Diel's original description the roots are referred to as napiform incrassate, suggesting a perennial habit.

CHIRIQUÍ: Pastures around Boquete, 100–1300 m, *Pittier 3364* (NY, US). Cerro Vaca, eastern Chiriquí, 900–1136 m, *Pittier* 5359 (US). Jarmillo, Boquete District, 4500 ft, *Terry 1273* (MO). COCLÉ: Hills N of El Valle, 800 m, *Allen* 2238 (MO). Picacho de Olá, 350–600 m, *Pittier 5069* (US—left hand specimen only).

7. CALCEOLARIA

ULF MOLAU*

Calceolaria L., Kongl. Vetensk. Akad. Handl. 31: 288, 1770. TYPE: *C. pinnata* L.

Fagelia Schwenke, Verh. Bataafsch Genootsch. Rotterdam 1: 147. 1774. TYPE: *F. flavicans* J. F. Gmel.

Annual or perennial *herbs* or *shrubs*. *Leaves* simple, opposite (ternate in some Peruvian species), petiolate or sessile. *Inflorescence* terminal or axillary, usually consisting of pairs of cymes, sometimes reduced to axillary pairs of pedicels. *Flowers* with the calyx 4-parted, the sepals valvate, the corolla bilabiate, yellow or reddish (Peru and Chile); upper lip usually smaller than the lower lip, hooded; lower lip saccate, inflated, globose; stamens 2, the filaments short, the anther cells deflexed or divaricate; ovary 2-loculed; the style short, often recurved, the stigma simple. *Capsule* dry; seeds minute, numerous.

Calceolaria includes about 300 species and is one of the largest genera of the Andes, ranging from Mexico to Cape Horn. In Central America, Venezuela, Colombia, Ecuador, Peru and Bolivia, the genus is restricted to mountain regions, occurring at elevations of 1000–4000 m. In Argentina and Chile, however, many lowland species occur, frequently with an acaulescent habit.

Four species are known to occur in Panama. *Calceolaria irazuensis* and *C. perfoliata* belong to the subgenus *Cheiloncos* (Wettst.) Pennell, comprising species with entire leaves and anthers with contiguous cells. Both anther cells are fertile and the connective is reduced. This subgenus consists of annual or perennial, mesophytic or xerophytic herbs and shrubs, and reaches its highest species diversity in Ecuador and Peru. *Calceolaria mexicana* and *C. tripartita* belong to the other subgenus, *Calceolaria*, which comprises usually widespread, hydrophytic annual herbs, characterized by pinnatifid-lobed leaves and peculiar anthers. The anther cells are separated by the elongated connective, and the lower one is often sterile and modified.

Literature:

Pennell, F. W. 1945. The genus *Calceolaria* in Southeastern Peru. Proc. Acad. Nat. Sci. Philadelphia 97: 174.

a. Leaves entire, the margin serrate; anther cells contiguous, both fertile, (subgenus *Cheiloncos*)
   b. Leaves sagittate or narrowly triangular; petioles broadly winged and connate at the base ..... 3. *C. perfoliata*

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bb. Leaves broadly lanceolate; petioles not dilated ..... 1. *C. irazuensis*
aa. Leaves usually deeply pinnatifid-lobed; anther cells separated by the elongated connective, the lower one fertile or sterile (subgenus *Calceolaria*)
c. Lower anther cell fertile ..... 2. *C. mexicana*
cc. Lower anther cell sterile ..... 4. *C. tripartita*

1. **Calceolaria irazuensis** Donnell Smith, Bot. Gaz. (Crawfordsville) 20: 292. 1895. TYPE: Costa Rica, *Donnell Smith 4904* (K).—FIG. 6.

C. costaricensis Kränzl., Ann. K. K. Naturhist. Hofmus. 22: 192. 1907. TYPE: *Endres* (B, not seen, destroyed).

Erect or scandent *herb* to 2 m tall; stems puberulent, distally tomentous with short brown or purplish hairs. *Leaves* 4.8–12 cm long, 1.7–4.3 cm broad, broadly lanceolate, apically acuminate, basally truncate or attenuate, sometimes narrowed almost to the base of the petiole, the margin irregularly serrate or serrulate, above dark green, glandular dotted and often short pilose, beneath paler, reticulate venose, the primary and the secondary veins tomentous with brownish hairs, the lamina glabrous, dotted with sessile yellowish glands; petiole 5–15 mm long, tomentous or villous. *Inflorescence* of 1–2 pairs of 2–10-flowered cymes; primary peduncles (3.5–)5–12 cm long, in vestiture resembling the stems; pedicels 0.8–4.0 cm, tomentous; bracts resembling the main leaves but smaller, subordinate bracts lacking. *Flowers* with the sepals 4.5–9.0 mm long, 3.5–7.0 mm broad, ovate, brownish green, both sides with yellowish hyaline glands, ciliate; corolla externally glandular papillose or glandular pilose at least around the mouth, the upper lip light yellow, 6–8 mm long, 10–13 mm broad, hooded, flattened in the lateral view, the lower lip deep yellow, 15–25 mm long, 10–17 mm broad, projecting, saccate about ⅜ of its length, internally with a tuft of white hairs below the base and between the stamens; anthers 3.5–4.0 mm long, dark brown, dehiscing throughout, the cells divaricate, equal, their distal parts bent somewhat downward, the filaments 1.5 mm long, glabrous; ovary glandular, style 4–5 mm long, distally decurved. *Capsule* 5–8 mm long, globose, with small glands and a slightly pointed apex.

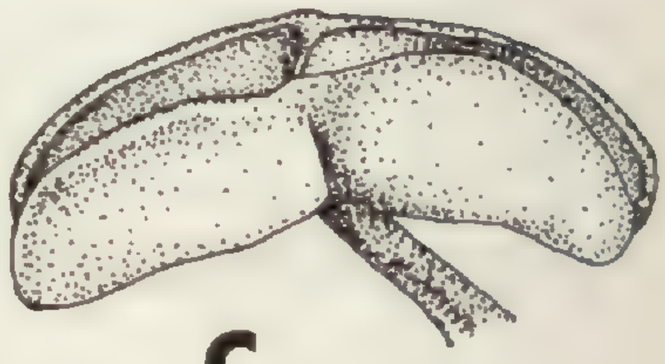
Calceolaria irazuensis is readily distinguished from other Central American species of the genus by shape of leaves and corolla. It belongs to the section *Dermatophylla* Pennell, which ranges from Costa Rica to Peru. It is an upland species, restricted in its distribution to the higher mountains of Panama and Costa Rica.

CHIRIQUÍ: Valley of the upper Río Chiriquí Viejo, *White 115* (MO). E slope of Volcán de Chiriquí (Barú) above Boquete, 3100 m, *Davidse & D'Arcy 10280* (MO). Loma Larga to summit, Volcán de Chiriquí, 2500–3380 m, *Woodson et al. 1061* (MO). Potrero Muleto to summit of El Barú, *D'Arcy 10161* (MO). Alto Respinga and above, 2800 m, *D'Arcy 9995* (MO).

2. **Calceolaria mexicana** Benth., Pl. Hartw. 47, 1840. TYPE: Mexico, *Hartweg 356* (K).—FIG. 6.

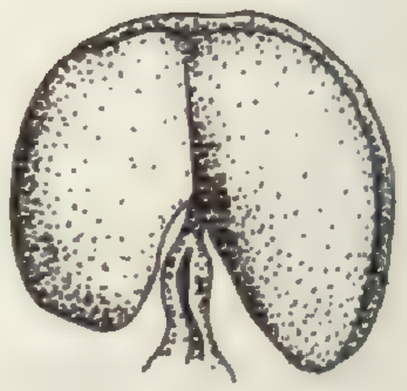
C. glutinosa Heer & Regel, Linnaea 24: 196. 1851. TYPE: Guatemala, *Warscewicz* (not seen).
C. urticina Kränzl., Feddes Repert. Spec. Nov. Regni Veg. 1: 82. 1905. TYPE: Mexico, *Uhde 1203* (not seen).

E



C

F



D

B

A

FIGURE 6. *Calceolaria*.—A–C. *Calceolaria irazuensis* Donnell Smith.—A. Flowering branch (×7/10).—B. Flowers (×7/10).—C. Stamen (×10⅘). [A & C after *Davidse & D'Arcy 10280* (MO); B after photo of *D'Arcy 9995* (MO).]—D. *Calceolaria perfoliata* L.f. Stamen (×10⅘). [After *D'Arcy* (MO-2338343).]—E. *Calceolaria tripartita* Ruiz & Pavón (×10⅘). [After *Woodson & Schery 701* (MO).]—F. *Calceolaria mexicana* Benth. (×10⅘). [After *D'Arcy 6421* (MO).]

C. palustris Sodiro ex Kränzl., Pflanzenreich 4 (257c): 27. 1907. TYPE: Ecuador, *Sodiro 115 1 bis* (B, not seen, destroyed; photo PH).

C. prostrata Kränzl., Feddes Repert. Spec. Nov. Regni Veg. 1: 31. 1907. TYPE: Venezuela. *Ernst* (BM).

Fagelia crenatiloba Pennell, Proc. Acad. Nat. Sci. Philadelphia 72: 182. 1920. TYPE: Colombia, *Pennell 3119* (NY).

F. micrantha Pennell, Proc. Acad. Nat. Sci. Philadelphia 72: 180. 1920. TYPE: Colombia. *Pennell 3145* (NY).

F. radiculoides Pennell, Proc. Acad. Nat. Sci. Philadelphia 72: 181. 1920. TYPE: Colombia. *Pennell 1942* (NY; isotype PH).

C. laciniata Kränzl., Repert. Spec. Nov. Regni Veg. 27: 3. 1929. TYPE: Colombia, *Schultze* (B, not seen, destroyed).
C. radiculoides (Pennell) Kränzl., Repert. Spec. Nov. Regni Veg. 27: 4. 1929.
C. flosparva Edwin, Phytologia 19: 380. 1970. TYPE: Peru, *Pennell 15633* (PH, holotype; F, US isotypes).

Annual *herb*, 0.1–0.5(–1.0) m tall; stems procumbent or ascending, fleshy, pilose with fine, often glandular hairs. *Leaves* 2–6(–11) cm long, 1.5–5(–6.5) cm broad, very variable, usually pinnatisect and ovate, occasionally almost entire and then lanceolate and incised, serrate, basally truncate or attenuate, lateral lobes in 1–2(–3) pairs, usually lingulate, acute or obtuse, the margin doubly serrate, occasionally laciniate, above green, pilose, beneath pale, glabrous or pilose on the midrib; petioles 1–6 cm long, often slightly winged distally, connate by a swollen ridge across node. *Inflorescence* varying from axillary pairs of pedicels to terminal, repeatedly dichotomous 5–30-flowered cymes; primary peduncles 1.5–9 cm long; pedicels 1–3 cm long, pilose or villose, often with gland-tipped hairs; bracts petiolate, entire, lanceolate, acute, the margin serrate; subordinate bracts frequently present. *Flowers* with the sepals 3–7 mm long, 1.5–3 mm broad, green, lance ovate, acute or acuminate, glabrous or puberulous, the margin denticulate; corolla small, sulphur yellow, glabrous, the upper lip 1–2 mm long, 2–3 mm wide, hooded, concealing the anthers, the lower lip 5–11 mm long, 3–6 mm wide, projecting, saccate most of its length, the proximal part appressed against the upper lip and closing the mouth; anthers 2.0–3.5 mm long, both cells fertile, much shorter than the elongated, linear connective; style 0.5–1.5 mm long, slightly curved. *Capsule* 3–9 mm long, broadly ovoid, glandular-pilose.

This species is best recognized by its anthers, which have both cells fertile and separated by the elongated connective. *Calceolaria mexicana* is a common upland species of moist and wet places, ranging from Mexico to Bolivia.

BOCAS DEL TORO: Robalo Trail, N slope of Cerro Horqueta, (6–7000 ft), *Allen 4909* (MO, P). CHIRIQUÍ: Río Chiriquí Viejo just above Guadelupe, *Croat & Porter 16038* (MO). Las Nubes 2.7 mi NW of Río Chiriquí Viejo W of Cerro Punta, 2200 m, *Croat 22389* (MO). La Popa above Boquete, 5200 ft, *D'Arcy 6421* (C, MO). Gravel bar in Río Chiriquí Viejo across from town of Cerro Punta, 1830 m 6000 ft, *D'Arcy 6592* (C, MO). Alto Respinga and above, 2800 m, *D'Arcy 9974* (MO). Bajo Chorro, Boquete District, 6000 ft; clearing in rain forest, *Davidson 139* (MO). Boquete trail, Cerro Respinga, E of town of Cerro Punta, 2000–2500 m, *Gentry 5902* (MO). Valley of upper Río Chiriquí Viejo, Monte Lirio, 1300–1900 m, *Seibert 168* (MO). Trail between Cerro Punta and Quebrada Bajo Grande, 2000–2100 m, *Wilbur et al. 11886* (MO). 2 km W of La Garita 3 km WNW of Cerro Punta, 2000 m, *Wilbur et al. 15254* (MO). Bajo Chorro, 1900 m, *Woodson & Schery 622, 636, 642* (all MO).

3. **Calceolaria perfoliata** L. f., Suppl. 86, 1781. TYPE: Colombia, *Mutis 121* (LINN, holotype, isotypes PH, S, US).—FIG. 6.

Fagelia perfoliata (L.f.) Kuntze, Rev. Gen. Pl. 2: 460. 1891.
F. tolimensis Pennell, Proc. Acad. Nat. Sci. Philadelphia 72: 177. 1920. TYPE: Colombia, *Pennell 2979* (NY).
Calceolaria homoiclada Kränzl., Repert. Spec. Nov. Regni Veg. 27: 10. 1929. TYPE: Colombia, *Schultze* (B, destroyed, not seen).

Scandent *herb* 1–4 m long; stems usually purplish, pilose, with long internodes. *Leaves* joined by the connate petioles; leaf-blades sagittate or narrowly triangular, 6–11 cm long, 3.5–7 cm broad, acute or somewhat acuminate, basally truncate or

slightly cordate, the margin irregularly doubly dentate or serrate, above green, pilose, beneath pale green or grayish green, reticulate venose, the nerves villous with whitish hairs, the lamina glabrous or pilose; petiole 2–5 cm long, winged, the margin entire or denticulate, at the connate base 2–4 cm broad, distally 0.5–1.5 cm broad. *Inflorescence* of 2–4 pairs of 10–20-flowered axillary cymes; peduncles 6–15 cm long; pedicels 1.5–4.5 cm long, villous with spreading whitish hairs; bracts oblique ovate, sessile, acuminate, dimidiate, irregularly dentate, 3–7 cm long, 2–4 cm broad, subordinate bracts lacking. *Flowers* with the sepals 9–12 mm long, 6–8 mm broad, somewhat enlarged during ripening of the capsule, yellowish, ovate, caudate acuminate, puberulent on both the surfaces, ciliate; corolla sulphur yellow, the upper lip paler, externally slightly pilose, the upper lip globose, arched over the anthers, 4–6 mm long, 6–9 mm broad, the lower lip inflated, projecting, finally pendent, 15–20 mm long, 8–15 mm broad, saccate to about ½ of its length; anthers dark brown, horseshoe shaped, the cells decurved laterally, each 2–3 mm long; filament glabrous, 1–2 mm; ovary covered with a villous tomentum; style almost straight, 5–7 mm long. *Capsule* 6–7 mm long, ovoid conic, puberulent.

Calceolaria perfoliata is recognized by its peculiar leaves and shape of the anthers. A related species, *C. trilobata* Hemsl., native of Colombia and Ecuador, has been introduced to Guatemala, but it has not been reported from Panama. It is distinguished from *C. perfoliata* by deltoid leaf-blades, green sepals and divaricate anther cells. Both species belong to the section *Zygophylla* Pennell, comprising herbs with perfoliate leaves, and ranging from Central America to Bolivia.

Calceolaria perfoliata is an upland species, ranging from Costa Rica to Ecuador and it is abundant in Colombia. In Panama it is restricted to the mountains of Chiriquí.

CHIRIQUÍ: Alto Respinga and above, 2800 m, *D'Arcy* (MO-2338343). Bajo Chorro, Boquete District, 1830 m, *Davidson 159* (MO). W slope of El Barú, 2130–2440 m, *Tyson & Loftin 5981* (MO). Potrero Muleto to summit, Volcán de Chiriquí, 3500–4000 m, *Woodson & Schery 445* (MO).

4. **Calceolaria tripartita** Ruiz & Pavón, Fl. Peruv. Chil. 1: 14, *tab.* 22. 1798. TYPE: Peru, *Pavon* (not seen).—FIG. 6.

C. pinnata Ruiz & Pavón, Fl. Peruv. Chil. 1: 14, *tab. 19*. 1798. non L. TYPE: Peru, *Pavon* (MA).
C. heterophylla Willd., Enum. Pl. Hort. Berol. 29. 1809. non R. & P. TYPE: Ecuador, *Bonpland* (B-Willd.).
C. chelidionoides H.B.K. Nov. Gen. Sp. Pl. 2: 378. 1818. TYPE: Ecuador, *Bonpland 2214*.
C. scabiosaefolia R. & S. in L., Syst. Veg. 1: 187. 1817. TYPE: Ecuador, *Bonpland* (B-Willd.). (B-Willd.; isotype P).
C. gracilis H.B.K., Nov. Gen. Sp. Pl. 2: 379. 1818. TYPE: Ecuador, *Bonpland 3109* (B-Willd.; photo F, PH).
C. chelidonioides flaccida Benth. in DC., Prodr. 10: 204. 1846. TYPE: Ecuador, *Hall 3* (K).
C. chelidonioides parvifolia Benth. in DC., Prodr. 10: 204. 1846. TYPE: Ecuador, *Hartweg 1271* (K).
Fagelia chelidonioides (H.B.K.) Kuntze, Rev. Gen. Pl. 2: 459. 1891.
F. scabiosaefolia (R. & S.) Kuntze, Rev. Gen. Pl. 2: 460. 1891.

Calceolaria ranunculoides Kränzl., Feddes Repert. Spec. Nov. Regni Veg. 1: 97. 1905. TYPE: Peru, *Weberbauer 2708* (not seen).
C. rivularis Kränzl., Feddes Repert. Spec. Nov. Regni Veg. 1: 83. 1905. TYPE: Bolivia, *Fiebrig 3394* (BM).
C. sarmentosa Kränzl., Feddes Repert. Spec. Nov. Regni Veg. 1: 97. 1905. TYPE: Peru, *Weberbauer 3121* (not seen).
C. mandoniana Kränzl., Pflanzenreich. 4(257c): 30. 1907. TYPE: Bolivia, *Mandon 460* (BM).
Fagelia diversifolia Pennell, Addisonia 4: 73, pl. 157. 1919. TYPE: Colombia, *Pennell 1320* (NY).
F. pinnatisecta Pennell, Proc. Acad. Nat. Sci. Philadelphia 72: 185. 1920. TYPE: Colombia, *Rusby & Pennell 721* (NY).
F. scalaris Pennell, Proc. Acad. Nat. Sci. Philadelphia 72: 184. 1920. TYPE: Colombia, *Rusby & Pennell 710* (NY).
Calceolaria puru-puru Kränzl., Feddes Repert. Spec. Nov. Regni Veg. 27: 2. 1929. TYPE: Peru, *Herrera 748* (B, destroyed; photos F, PH).
C. gracilis stenoptera Diels, Biblioth. Bot. 116: 140. 1937. TYPE: Ecuador, *Diels 848* (not seen).
C. obscura Pennell, Proc. Acad. Nat. Sci. Philadelphia 97: 176, *fig 16a.* 1945. TYPE: Peru, *Pennell 14043* (PH, holotype; isotypes BM, F, GH, NY, US).
C. tripartita mandoniana Pennell, Proc. Acad. Nat. Sci. Philadelphia 97: 175. 1945.
C. cantensis Guillen, Raymondiana 1: 37. 1968. TYPE: Peru, *Guillen 3306* (SMF).
C. soukupii Guillen, Raymondiana 1: 34. 1968. TYPE: Peru, *Guillen 3528* (SMF).
C. velardei Guillen, Raymondiana 1: 41. 1968. TYPE: Peru, *Infantes 1273* (SMF).
C. celendinensis Guillen, Raymondiana 2: 16. 1969. TYPE: Peru, *Riccio 6279* (SMF).
C. grandepinnata Edwin, Phytologia 19: 380. 1970. TYPE: Peru, *Pennell 14891* (US, holotype; isotypes GH, NY, PH, US).

Annual *herb*, 0.1–0.7 m tall; stems procumbent or ascending, fleshy, often reddish below, pilose with fine, often glandular hairs. *Leaves* (1.5–)3–8(–20) cm long, (1.2–)3–7.5(–15) cm broad, very variable, pinnatisect, ovate with 1–3 pairs of elliptic or lanceolate, acute lateral lobes, the apical lobe ovate or lanceolate, usually somewhat larger than the others, doubly serrate, occasionally incised laciniate, above green and pilose, often with gland-tipped hairs, beneath pale green, pilose or almost glabrous; petioles (0.6–(2–5)–6) cm long, at the lower nodes connate by a swollen ridge across the node. *Inflorescence* usually of several pairs of axillary pedicels, sometimes a terminal pair of 6–12 flowered cymes; primary peduncles 3–8 cm long; pedicels 1–3 cm long, glandular pilose; bracts, when present, petiolate, entire or nearly so, lanceolate, acute, the margin serrate or laciniate; sepals 4–7 mm long, 2.5–4.0 mm broad in anthesis, later somewhat enlarged, green, ovate, acuminate, denticulate, ciliate with gland-tipped hairs; corolla yellow, sometimes with an orange tinge, glabrous, the upper lip 2–3 mm long, 3–4 mm wide, hooded, concealing the fertile parts of the anthers, the lower lip 10–20 mm long, 6–15 mm wide, projecting, saccate most of its length, the proximal part appressed against the upper lip, closing the mouth; anthers 2.0–3.5 mm long, the posterior (upper) cell fertile, the anterior (lower) cell sterile, reduced to a knob, projecting down in the orifice as a blunt club, by leverage bringing the posterior fertile cell from under the hood of the corolla, the connective elongated, slender and sigmoid, occasionally flattened, 1.2–2.0 mm long, the filament 0.5 mm long; style 1.5–2.0 mm long, curved. *Capsule* widely conic, 5–9 mm long, glandular pilose.

This species is superficially like *Calceolaria mexicana* but differs in having leaf lobes more deeply cut and the lower anther cell sterile. *Calceolaria tripartita*

shows a striking local variation, especially concerning shapes of leaves and lower anther cell. This is probably due to self-pollination, which occurs regularly in late anthesis, even though the flowers have an elaborate mechanism of cross-pollination, resembling that of *Salvia*.

The type collection of *Calceolaria tripartita* has evidently disappeared from Madrid (MA). The applicability of this name has been carefully considered by Pennell (1945). *Calceolaria tripartita* is an upland species, occurring on moist or wet soil and gravel. It ranges from Mexico to Chile and is one of the most common species of the genus in the northern Andes.

CHIRIQUÍ: Río Chiriquí Viejo just above Guadelupe, *Croat & Porter 16024* (MO). Top of peak between Baru and Respinga, 3000 m, *D'Arcy 10112* (MO). NW of Boquete, Cerro Horqueta, trail to lower edge of cloud forest, 5000–5800 ft, *Dwyer et al. 464* (MO). Río Caldera beyond Bajo Mono near Boquete, 1700 m, *Wilbur et al. 11049* (MO). Río Caldera beyond Bajo Mono about 4 mi NW of Boquete, 4200 ft, *Wilbur et al. 13497* (MO). Finca Lérida, 1750 m, *Woodson & Schery 234* (MO). Vicinity of Bajo Chorro, 1900 m, *Woodson & Schery 701* (MO). Bajo Mono, mouth of Quebrada Chiquero, along Río Caldera, 1500–2000 m, *Woodson et al. 997* (MO).

8. CAPRARIA

Capraria L., Sp. Pl. 628; Gen. Pl., ed. 5. 276. 1754. TYPE: *C. biflora* L.

Slender branched *shrubs* or *herbs*, the branching alternate. *Leaves* alternate, rotund or linear, mostly toothed in the apical ½, cuneate below, inconspicuously glandular punctate, the midvein prominent with about 3 ascending lateral veins on each side; petioles not distinct. *Inflorescences* 1–several flowers in the axils of a leaf; pedicels slender. *Flowers* with the calyx lobes 5, equal, narrow, separate to near the base, the corolla white, rotate or tubular campanulate, glabrous outside, sometimes bearded at the throat within, the stamens 4 or 5, subequal or not, the filaments glabrous, inserted low or high on the corolla tube, alternate with the corolla lobes, the anthers introrse, versatile, basifixed, the basal portions of the thecae divaricate; ovary ovate conical, the style slender, apically compressed, the stigma a pair of lateral areas on the style apex. *Capsule* elliptical, ovoid or conical, glandular punctate, dehiscent septicidally and loculicidally, the placenta remaining as a conspicuous, reticulate-pitted peg; seeds numerous, minute, yellow, with a thick crystalline reticulum.

Capraria is a genus of about 4 species of tropical and subtropical America, one species adventive in the Old World. On the basis of pollen morphology, Niezgoda & Tomb (1970) transferred this genus to the Myoporaceae.

Literature:

Niezgoda, C. J. & A. S. Tomb. 1975. Systematic palynology of tribe Leucophylleae (Scrophulariaceae) and selected Myoporaceae. Pollen et Spores 17: 497–516.

Sprague, T. A. 1921. A revision of the genus *Scoparia*. Kew Bull. 1921: 205–212.

a. Style 2 mm long; corolla rotate; calyx only about ½ as long as the capsule, narrowly deltoid ..... 2. *C. peruviana*

aa. Style 5 mm long; corolla campanulate or tubular; calyx about as long as the capsule, linear, narrow throughout ..... 1. *C. biflora*

1. **Capraria biflora** L., Sp. Pl. 628. 1753. TYPE: Cultivated, Uppsala (LINN 785.1, not seen; microfiche MO).—FIG. 7.

Slender branched *shrub* to 2 m tall, the twigs tomentulose to glabrate, often drying whitish, slender, the branching alternate. *Leaves* alternate, obovate to oblanceolate, apically obtuse, basally cuneate, toothed in the apical ½, the teeth mucronulate, not callose, the midvein prominent, with ca. 3 strongly ascending veins on each side, to 7 cm long, 1.5 cm wide; petiole obscure. *Inflorescence* of 1 or 2 flowers in the leaf axils, numerous; pedicels slender, mostly 1.0–1.5 cm long, glabrate to tomentose. *Flowers* inconspicuous, the calyx of 5 equal, linear lobes ca. 6 mm long, glabrate or hirsute, sometimes ciliate; corolla white, tubular campanulate, ca. 6–9 mm long, 5-lobed about ½ way down, the lobes rounded, subequal within, glabrous outside, 3 lobes bearded at the throat, sometimes glabrous; stamens 4 or 5, alternate with the corolla lobes, the filaments slender, glabrous, ca. 3 mm long, inserted at the base of the corolla tube, 2 slightly longer and basally geniculate, the anthers ca. 1 mm long; ovary obtuse conical, 2-sulcate, glabrous, the style ca. 5 mm long, slightly compressed apically, the stigma a linear region along the narrow sides of the style. *Capsule* ovoid, glabrous, glandular punctate, septicidally and loculicidally dehiscent, ca. 5 mm long; placenta persistent, conspicuously rugose punctate; seeds yellow, rugose, with a thick, crystalline reticulum, ca. 0.5 mm long.

Nearly all Panamanian collections of this species are from near beaches. It ranges from Florida to Argentina, and is adventive in the Old World. It is a frequent element of the Antillean flora. Several infraspecific taxa have been recognized in this species based on degree of pubescence. Most Panamian plants are glabrate, but a few collections are tomentulose and might be distinguished as forma *hirta* Loes.

This species is used to make a tea, used sometimes as a beverage and sometimes for reputed medical properties. In large doses it may be a dangerous depressant. "Goatweed," "Te del Pais," "Hierba Te," "Cola de Gallo."

BOCAS DEL TORO: Bocas runway area, *Lazor et al. 2305, 2387* (both SCZ). Isla Colón, *Wedel 509* (MO), *2977* (MO, US). Water Valley, *Wedel 1910* (US). CANAL ZONE: Fort San Lorenzo, *Burch et al. 1027* (UC). Farfan Beach, *Godfrey 1677* (SCZ). Gatún, *Heriberto 106* (US). Edge of mangrove swamp near Fort Randolph, *Standley 28594* (US). Fort Sherman near beach, *Standley 31209* (US). PANAMÁ: Taboga Island near beach, *Dwyer 2818A, 2819* (both MO). Main beach, San Jose Island, *Harlow 60* (US). Low woods E of Bella Vista, *Maxon & Valentine 6951* (US). Taboga Island, *Pittier 3533* (US). Bella Vista, *Standley 25323* (US). Punta Paitilla, *Standley 30798* (US). Taboga Island, *Woodson et al. 1492* (MO). SAN BLAS: Beach E of Puerto Obaldía, *Croat 16897* (MO).

2. **Capraria peruviana** Benth. in DC., Prodr. 10: 430. 1846. Based on Capraria peruviana, Agerati foliis absque pediculis, Feuillée, Obs. 2: 764, *tab. 123, fig. 48.* 1714.

Shrub to 2 m tall, the branches slender, puberulent, ridged below the nodes with concaulescent leaf tissue. *Leaves* alternate, lanceolate, apically acute, basally

FIGURE 7. *Capraria biflora* L. Habit (×3/5). [After *Harlow 60* (US).]

narrowed, denticulate in the upper ½, to 7 cm long, 10 mm wide; midvein prominent, the lateral venation obscure; petiole not evident. *Inflorescence* of 1–4 flowers in the axils of the leaves, numerous, the pedicels slender, puberulent, ca. 10 mm long. *Flowers* with the calyx of 5 equal lobes free nearly to the base, narrowly deltoid, ca. 3 mm long, glabrate; corolla white, rotate, ca. 4 mm long, the lobes acute, exceeding the tube, the tube shorter than the calyx lobes, glabrous outside, glabrate within; stamens 5, the filaments glabrous, unequal, 2 short, ca. 1 mm long, inserted near the top of the tube, 2 ca. 2 mm long inserted at the base of the tube; anthers versatile, 1 mm long, the thecae basally divaricate; ovary obtuse conical, the style 2 mm long, apically compressed, the stigma linear, following the style margins, ca. 1 mm long. *Capsule* 4–5 mm long, broadly ellipsoidal, glandular punctate, much exceeding the calyx lobes, the seeds yellow, ca. 0.4 mm long, reticulate.

This species is known from Peru and Ecuador, and it is sparingly found in Colombia and Panama. Close attention to detail is necessary to separate it from the more frequent and widespread *C. biflora*. The above description was made from a series of Ecuadorian collections at MO.

PANAMÁ: On old walls, Panama, *Hayes* 395 (K, not seen, cited by Sprague 1921).

9. CASTILLEJA

Noel H. Holmgren[5]

Castilleja Mutis ex L.f., Suppl. Pl. 47, 293. 1781. TYPE: *C. fissifolia* L.f.

Perennial or annual *herb*, often becoming shrubby in warm regions, hemiparasitic. *Leaves* alternate, sessile, entire or pinnately lobed, cauline. *Inflorescence* a short or elongate spike or raceme; bracts often leaflike at the base of the inflorescence, gradually differentiating upward, often more conspicuously colored than the flowers. *Flowers* conspicuous to inconspicuous, mostly concealed behind the bracts; calyx tubular, equally or unequally cleft into 4 segments, usually partially united into 2 lateral primary lobes or the primary lobes entire by complete fusion of the lateral clefts, somewhat accrescent in fruit; corolla greenish or the exserted parts often colored, tubular, elongate and narrow, bilabiate, the upper lip galeate (hooded), beaklike, the lobes united to the tip and enclosing the anthers, the lower lip somewhat 3-saccate with 3 more or less rudimentary teeth or sometimes 3 petaloid lobes nearly equalling the galea in length, external to the upper lip in bud; stamens 4, didynamous, attached near or above the middle of the corolla tube, the 2 anther-sacs unequally placed, the outer longer and attached by its middle, the inner smaller and suspended from its apex; stigma united and capitate, or sometimes slightly 2-lobed. *Fruit* a loculicidal capsule, more or less asymmetrical, ovate to globose; seeds numerous, the loose testa alveolately reticulate. $x = 12$.

Castilleja includes about 200 species. They occur chiefly in western North America, but are represented in eastern North America with 3 species, northern Asia with about 5, Central America with about 8, and Andean South America

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with about 5. The major taxonomic distinctions are in the flowers. Named in honor of Domingo Castillejo, a botanist of Cadiz, Spain.

Literature:

Pennell, F. W. 1940. Scrophulariaceae in R. E. Woodson, Jr. & R. W. Schery, Contributions toward a flora of Panama. Ann. Missouri Bot. Gard. 27: 338–341.

a. Inflorescence spicate with small, crowded flowers; calyx subequally cleft both front and rear; plants annuals ..... 1. *C. arvensis*
aa. Inflorescence racemose and secund with conspicuous flowers; calyx much more deeply cleft in front than in back; plants perennials ..... 2. *C. quirosii*

1. **Castilleja arvensis** Schlecht. & Cham. Linnaea 5: 103. 1830. TYPE: Mexico, near Jalapa, *Schiede & Deppe* (not seen).

C. communis Benth. in DC., Prodr. 10: 529. 1846. LECTOTYPE: Mexico, Vera Cruz, Jalapa, *Linden 212* (not seen, photo NY), designated by Pennell.
C. communis fo. *johnstoniae* Standley, Publ. Field Mus. Nat. Hist., Bot. Ser. 23: 86. 1944. TYPE: Guatemala, Santa Lucía Cotz, *Standley 63500* (F).
C. agrestis Pennell, Fieldiana, Bot. 28(3): 519. 1953. TYPE: Mexico, Michoacán, Pátzcuaro, *Pringle 3349* (PH).

Annual *herb*; stems 1–8 dm tall, usually simple, sometimes sparingly branched above, often with fleshy leaf scales (tubercles) at the base; herbage villous to hirsute, usually with viscid and gland-tipped hairs. *Leaves* 3–6(–10) cm long, 5–15(–22) mm broad, entire, oblanceolate or narrow lanceolate to elliptic or obovate, usually tapering to a petiolar base, the midvein and usually 2 lateral veins prominent, the larger leaves irregularly pinnately veined. *Inflorescence* a dense, many flowered spike, glandular villous; bracts lanceolate to oblanceolate, tipped with red to orange or occasionally yellow. *Flowers* small; calyx 9–12 mm long, the median cleft subequal, 3–5 mm deep, the primary lobes entire, truncate or rounded, viscid villous below, densely glandular puberulent on the rigid lobes, distally colored as on the bracts; corolla included in the calyx, usually about 1 mm shorter to as long as the calyx, the galea 2.5–5 mm long, the lower lip much reduced with 3 lanceolate lobes, the tube longer than the galea, 6–8.5 mm long. *Fruit* a capsule, 5–7 mm long, round, obovoid spherical, often blackish brown; seeds numerous, elongate, truncate at the summit.

Castilleja arvensis is the most widespread species of *Castilleja*, ranging from central and northeastern Mexico south through Central America to nearly throughout South America, and it has been introduced to Hispañola and Hawaii. It most commonly occurs in disturbed areas such as pastures, cornfields, roadsides and open forests from near sea level to about 2500 m elevation, and it flowers year-round.

CHIRIQUÍ: Cerro Punta, 2000 m, *Allen 1557* (MO, NY, US). Burica Peninsula, Rabo de Puerco, 8 km W of Puerto Armuelles, 150 m, *Busey 451* (MO). Camino entre Bambito y La Amenaza, 6000 ft, *Correa 1297* (PMA). Methodist Camp near Nueva Swissa, *Croat 13523* (MO). 1 mi E of Cañas Gordas, near Costa Rican border, *Croat 22317* (MO). Las Cumbres, N of Quebroad Iglesia, near town of Cerro Punta, *Croat & Porter 16100* (MO). Slope of La Popa above Boquete, 5400 ft, *D'Arcy & D'Arcy 6407* (MO). Across Río Chiriquí Viejo from town of Cerro Punta, *D'Arcy & D'Arcy 6524* (MO). Bajo Mono, Boquete District, 4500 ft,

Davidson 502 (MO). Cerro Respinga, E of town of Cerro Punta, 2000–2500 m, *Gentry* 5922 (MO). El Boquete, 1300 m, *Killip 3509* (US); *Maurice 700* (US). 2.5 km SE of town of Cerro Punta, *Mori & Kallunki 5642* (MO). Bajo Grande, 1–3 km E of town of Cerro Punta, 2000–2200 m, *Nee 9985* (MO). Around Boquete, 1000–1300 m, *Pittier 2851* (US). Cerro Punta, 6800 ft, *Ridgway & Solís 2410* (MO). 2 mi W of Cerro Punta, across the river, 6000 ft, *Tyson 7176* (PMA). Valley of the upper Río Chiriquí Viejo, 1300–1900 m, *White & White* 32 (MO). Finca Lérida to Peña Blanca, 1750–2000 m, *Woodson & Schery 291* (MO). Vicinity of Bajo Mona and Quebrada Chiquero, 1500 m, *Woodson & Schery 527* (MO). Boquete, 1200–1500 m, *Woodson & Schery 801* (MO).

2. **Castilleja quirosii** Standley, Publ. Field Mus. Nat. Hist., Bot. Ser. 18: 1104. 1938. TYPE: Alrededores del cráter del Volcán de Irazú, *Quiros* 329 (F).—FIG. 8.

C. aurantiaca Pennell, Ann. Missouri Bot. Gard. 27: 338. 1940. TYPE: Panama, *Woodson et al. 926* (MO, NY, PH).

C. chiriquiensis Pennell, Ann. Missouri Bot. Gard. 27: 338. 1940. TYPE: Panama, *Maxon 5307* (NY, US).

C. seibertii Pennell, Ann. Missouri Bot. Gard. 27: 339. 1940. TYPE: Panama, *Woodson et al. 1085* (MO, NY).

C. bicolor Pennell, Ann. Missouri Bot. Gard. 27: 340. 1940. TYPE: Panama, *Woodson et al. 1035* (NY, PH).

Perennial *herb* or *shrub*; stems 1.5–10 dm tall, simple or usually much branched and woody below, hirsute with spreading or reflexed hairs, rarely nearly glabrous, obscurely lined or ribbed by decurrent leaf bases. *Leaves* 1–3(–4) cm long, divided into 1–2(–4) pairs of lateral lobes in the upper ½ or rarely entire, the midblade linear, the lateral lobes filiform, usually 3-veined, densely and finely cinereous puberulent, sometimes nearly glabrous with scabrid margins and nerves. *Inflorescence* a secund raceme; bracts entire or the lower lobed, the pubescence as on the leaves, distally or nearly wholly colored red to orange; pedicels ascending, 2–6(–11) mm long in flower, 6–8(–18) mm long in fruit. *Flowers* conspicuous; calyx 15–20(–23) mm long, the posterior cleft shallow, 1–3 mm deep, the anterior cleft 11–16 mm deep, the primary lobes entire or emarginate, if lobed the posterior lobes longer, rounded, hispidulous, red to orange, sometimes yellowish orange at the tip; corolla (18–)22–28(–32) mm long, decurved, the galea more than twice as long as the tube, 16–20(–23) mm long, slender, densely white puberulent dorsally, yellow to yellowish green with reddish margins, the lower lip much reduced with 3 narrow teeth about 1 mm long, dark green or reddish green, the tube 7–8(–10) mm long. *Fruit* a capsule, 8–12 mm long, ovoid, dark brown.

Castilleja quirosii is frequent to rare in the upland of the Volcán de Chiriquí on open rocky ridges and in elfin forests from 2,000 to 3,600 m elevation, flowering year-round. It is also found on the slopes of Volcán de Irazú and Cerro de Escazú in Costa Rica, from 1,500 to 3,300 m elevation.

Pennell (1940), who described four new species from the slopes of Volcán Chiriquí, had only six collections from which to draw his conclusions. With 13 new collections from the Chiriquí Province for comparison the four Pennell entities merge into one variable species. The different growth forms Pennell distinguished appear to be phenotypic products of differing exposures to sun and wind, elevations and moisture. Pennell also distinguished the four on color

FIGURE 8. *Castilleja quirosii* Standley.—A. Habit (×⅕).—B. Flower (×1⅗). [After *Davidse & D'Arcy 10247* (MO).]

differences, but color variability is common in species of *Castilleja*. Standley based his *C. quirosii* on a collection from a disjunct population of the species in the Cordillera Central of Costa Rica.

Castilleja quirosii belongs to section *Castilleja*, a highly derived group that reaches its best development in the mountains of southern Mexico, Central America and northern Andean South America. The closest relatives to *C. quirosii* are in Costa Rica, *C. talamancensis* N. Holmgren of the northern half of the Cordillera de Talamanca and *C. irasuensis* Oerst. of Volcán Irazú and Volcán Turrialba in the Cordillera Central. These two kindred species differ from our species in having prominently ribbed stems and glabrate to glabrous herbage as opposed to obscurely ribbed, hispid stems. The calyx of *C. talamancensis* is red with yellow lobe tips while both *C. quirosii* and *C. irasuensis* are red or orange to the tips.

CHIRIQUÍ: Summit and SW face of Cerro Copete, 9000 ft, *Allen 4886* (MO). Top of peak between Barú and Respinga, 3000 m, *D'Arcy 10084* (MO). 11 km WNW of Boquete, 3000 m, *Davidse & D'Arcy 10247* (MO). Volcán de Chiriquí, Boquete District, 7000 ft, *Davidson 869* (MO). Potrero Muleto, Volcán de Chiriquí, Boquete District, 10400 ft, *Davidson 1032* (US). Summit of Chiriquí Volcano, 3600 m, *Killip 3600* (US). Cuesta Grande, E slope of Chiriquí Volcano, 2600–2990 m, *Maxon 5307* (NY, US). Upper belt of Chiriquí Volcano, N slope, 3000–3374 m, *Pittier 3088* (US). Volcán de Chiriquí, *Sapper* (US). Volcán de Chiriquí, Boquete District, 11,000 ft, *Terry 1353* (MO). 8 mi NE of El Volcán, 8100–8400 ft, *Tyson 834* (MO). Top of El Barú above 11,000 ft, *Tyson & Loftin 6162* (MO). Valley of the upper Río Chiriquí Viejo, *White 50* (MO). Finca Lérida to Peña Blanca, 1750–2000 m, *Woodson & Schery 332* (MO). Potrero Muleto to summit, Volcán de Chiriquí, 3500–4000 m, *Woodson & Schery 396* (MO), *431* (MO). Casita Alta, Volcán de Chiriquí, ca. 1500–2000 m, *Woodson, Allen & Seibert 926* (MO, NY). Loma Larga to summit, Volcán de Chiriquí 2500–3380 m, *Woodson et al. 1035* (MO, NY), *1085* (MO, NY).

10. DIGITALIS

Digitalis L.[6], Sp. Pl. 621. 1753; Gen. Pl., ed. 5. 272. 1754. TYPE: *D. purpurea* L.

Perennial *herbs* or rarely *shrubs*, sometimes scapose. *Leaves* alternate, simple, mostly crenate or dentate, apparently petiolate. *Inflorescences* terminal racemes, sometimes secund; pedicels basally bracteate. *Flowers* showy, calyx divided to the base, the 5 lobes alike; corolla yellowish, purplish, often spotted, conspicuously exserted, zygomorphic, campanulate, mostly pubescent; stamens 4, alike, the anthers with 2 similar thecae; style slender, elongate, the stigma 2-lobed. *Capsule* ovoid to conical, septicidal.

Digitalis is a genus of about 30 species of Europe and Asia. Several species are cultivated in other countries for ornament, and the species treated here is naturalized in many countries of the New World. "Foxgloves."

Literature:

Heywood, V. H. 1972. *Digitalis in* T. G. Tutin et al., eds. Flora Europaea 3: 239–241.

[6] A number of generic synonyms are given by Werner, 1960. Only the above name has been used for Panamanian plants.

Werner, K. 1960. Zur Nomenklatur und Taxonomie von *Digitalis* L., Bot. Jahrb. Syst. 79: 218–254.

1. **Digitalis purpurea** L.[7], Sp. Pl. 621. 1753. TYPE: Herb. Linn. (LINN 775.1, not seen, microfiche MO).—FIG. 9.

Perennial *herbs* to 1.5 m tall, stems sometimes stout, glabrate or scurfy pubescent with greyish arachnoid hairs, drying sulcate. *Leaves* alternate, 8–15 cm long (lower leaves sometimes much larger), elliptical or obovate, apically acute, obtuse or rounded, basally obtuse, narrowed into the winged petiolar area, the margins crenate serrate with numerous blunt teeth, pinnately veined with ca. 4 veins on each side, glabrate above, pilose beneath with whitish hairs, especially on the veins; petiole winged, 5–15 mm wide, 3–8 cm long, often exceeding the blades, basally clasping and concaulescent on the stem. *Inflorescence* a secund raceme to 30 cm long, the numerous flowers evenly spaced, the peduncle pilose or glabrate, the pedicels pilose, ca. 1 cm long, subtended by an ovate, pubescent bract. *Flowers* showy, fragrant, the calyx 5-lobed to the base, the lobes oblong, elliptical or ovate, apiculate, 12–18 mm long, glabrous to pubescent; corolla broadly campanulate, 3–5 cm long, somewhat zygomorphic with 4 short lobes, the lowermost slightly longer and deltoid, purple with brownish flecks on the lower side, glabrous outside, ciliolate, sparingly long pilose at the mouth within; stamens 4, straight, stout, the anthers alike, the thecae subequal, divaricate, basally connate, ovate, ca. 2 mm long; style slender, the stigma 2-lobed. *Capsule* ovoid conical, 12 mm long, 10 mm broad at the base, dehiscing septicidally, subtended by the wide-spreading calyx.

Digitalis purpurea is an Old World species widely planted for ornament. It is naturalized in Central America and has been collected in upland Chiriqui Province. Two variants are present in Panama, one with glabrate stems and calyces and acute leaves, the other (*Tyson 7211*) with short-pilose stems, calyces and rounded or obtuse leaves. The leaves and sap of this species are toxic and have caused deaths in humans and livestock. The drug digitalis is employed in medicine for the treatment of heart irregularities. "Foxglove"; "Dedalera."

CHIRIQUÍ: Alto Respinga, above Cerro Punta, around 3000 m, *D'Arcy 10680* (MO). Slopes of Cerro Punta, 2000 m, *Gentry 5891* (MO). Boquete trail 6 mi E of Cerro Punta, 7000 ft, *Tyson 7211* (PMA).

11. ESCOBEDIA

Escobedia Ruiz & Pavón, Fl. Peruv. Chil. Prodr. 91, *tab. 18*. 1794. TYPE: *E. scabrifolia* R. & P. = *E. grandiflora* (L.f.) Kuntze.

Silva Vell., Fl. Flum. 55. 1825. TYPE: S. *curialis* Vell. = *Escobedia grandiflora* (L.f.) Kuntze.
Micalia grandiflora Raf., Fl. Tell. 2: 104. 1836 [1837]. TYPE: *M. grandiflora* L.(f.) Raf.

Tall *herbs*, the stems relatively slender, drying sulcate, glabrous or scabridulous pubescent; roots orange. *Leaves* opposite, ovate to linear, coriaceous, scabrous,

[7] A number of synonyms are given by Werner, 1960. Only the above name has been used for Panamanian material. Werner also presented a number of infraspecific taxons.

FIGURE 9. *Digitalis purpurea* L. Habit (×½). [After *Tyson 7211* (MO).]

at least above, digitately nerved. *Inflorescences* of solitary or geminate flowers in the axils of upper leaves, sometimes aggregated into racemes or panicles; peduncles stout, bibracteate in the upper ½. *Flowers* showy, the calyx tubular, 5 or 10 nerved, apically 3–6 lobate, the lobes sometimes irregular, corolla tubular salverform, the tube long and slender, the limb spreading with 5 rounded lobes; stamens 4, the filaments inserted ½ way up the tube, ciliate, the anthers long

sagittate, included; style bent apically, the stigma running along one side or the style apex. *Capsule* included, the seeds relatively large.

The showy tubular flowers of this genus resemble those of *Brunfelsia undulata* (Solanaceae) or *Posequeria latifolia* (Rubiaceae) which are also fragrant night bloomers adapted to hawk moth pollination. The roots of *Escobedia* are used by local peoples as a food coloring agent which resembles saffron. "Color"; "Azafran."

Although Pennell recognized 15 species in the genus, there are fewer than six. In upper Central America, *Escobedia laevis* Cham. & Schlecht., a species with linear leaves and narrow calyces, occurs in marshes, but it has not been found as far south as Panama. Species with broader leaves often occur in drier habitats from Mexico to Paraguay and Brazil. The genus is closely related to the African genus *Cycnium* Mey. ex Benth. (1846) from which it may not be distinct. *Cycnium* has been distinguished by the anthers having one theca reduced.

Literature:

Pennell, F. W. 1931. *Escobedia*—A neotropical genus of the Scrophulariaceae. Proc. Acad. Nat. Sci. Philadelphia 83: 411–426.

Thieret, J. W. 1960. The Scrophulariaceae-Buchnereae of Central America. Ceiba 8: 92–101.

1. **Escobedia grandiflora** (L.f.) Kuntze, Rev. Gen. Pl. 3(2): 231. 1893.—FIG. 10.

Buchnera grandiflora L.f., Suppl. Pl. 287. 1781. LECTOTYPE: Colombia, *Mutis* (LINN 790.2, not seen; microfiche MO).

Escobedia scabrifolia Ruiz & Pavón. Syst. Veg. Fl. Peruv. Chil. 159. 1798. TYPE: Peru, *Pavón*, not seen.

Silva curialis Vell., Fl. Flum. 55; 1: *tab. 149*. 1825. TYPE: not seen.

Micalia grandiflora (L.f.) Raf., Fl. Tell. 2: 104. 1837.

Escobedia curialis (Vell.) Pennell, Proc. Acad. Nat. Sci. Philadelphia 83: 417. 1931.

Escobedia longiflora Pennell, Proc. Acad. Nat. Sci. Philadelphia 83: 423. 1931. TYPE: Mexico, *Pringle 6665* (MO).

E. reticulata Pennell, Proc. Acad. Nat. Sci. Philadelphia 83: 420. 1931. TYPE: Costa Rica, *Pittier 11118* (US).

Tall, perennial *herbs*; stems relatively slender, drying many sulcate, retrorsely scabridulous; roots conspicuously orange. *Leaves* opposite, ovate to narrowly deltoid, apically acute or obtuse, basally obtuse, truncate or slightly auriculate, the margins serrate with low, callose teeth, veins 5–7-digitate, impressed above, prominent beneath, the minor venation prominent beneath, stiffly coriaceous, scabrous with short, sturdy hairs on multicellular bases, the bases sometimes giving a pustulate appearance; petioles to 1 mm long or wanting. *Inflorescences* solitary, often geminate flowers in the upper leaf axils, sometimes aggregated

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FIGURE 10. *Escobedia grandiflora* (L.f.) Kuntze. Habit (×⅕). [After *Woodson & Schery 727* (MO).]

L. Mourrides

into a raceme; peduncles stout, curved, scabrous, 1.5–3.0 mm long bearing 2 opposite ovate to linear bracts to ca. 7 mm long on the upper ½. *Flowers* with the calyx tubular, 3–5 cm long, with 3–6 irregular deltoid lobes 5–8 mm long, conspicuously 10-nerved in the lower ½, 5 or 10 nerved apically, glabrous to scabrous, sometimes pubescent only on the veins, sometimes appearing pustulate with hair bases; corolla white, tubular salverform, the tube slightly curved, 8–10 cm long, 8–15 mm wide near the apex, the limb spreading 3–6 cm across with 5 rounded lobes, puberulent outside and on the limb with short gland-tipped hairs, glabrous within the tube; stamens 4, the filaments slender, compressed, inserted about ½ way up the tube, ca. 1.5 mm free, ciliate apically, the anthers alike, narrow, long sagittate with slender tails, 1.5 cm long, situated ca. ⅔ way up the tube, dehiscing by long, introrse slits, minutely apiculate; ovary narrow, glabrous, the style bent apically, pubescent at the stigmatic level, the stigma ca. 1.5 mm long, running along 1 side of the style, the final 5–7 mm sharply curved, enlarged, situated just above the anther tips. *Capsule* ca. 2 cm long; seeds 4.0–4.5 mm long.

Escobedia grandiflora is distinctive in its large, white, tubular salverform flowers and scabrous, coriaceous leaves. It has been collected only twice in Panama, perhaps because it blooms at an inconvenient collecting hour. Both collections are from Boquete, one of these noted as being a swampy meadow. In other countries it often occurs on drier sites such as cliff faces and wooded slopes.

Pennell and Thieret both applied the name *E. reticulata* to material from Panama and Costa Rica, which they distinguished by the pustulate calyces and the position and size of the bracts. While these characters may mark a local variant in a wide ranging species, they are not of significance at the species level. Pennell applied the name *E. curialis* to plants with wider leaves than is usual in northwestern South America. Although this may represent a distinct species, the plant illustrated by Vellozo, which is taken to be the type, has narrower leaves quite like those of plants from Panama. *Escobedia longiflora* was separated by Pennell and Thieret on the basis of the 10-ribbed calyx. In all species of *Escobedia* the calyces are 10-ribbed basally, and in *E. grandiflora* whether the intermediate set of ribs continues to the top of the calyx seems to vary within populations.

Although roots of this species are used for culinary purposes in other countries, no such use is known for Panama.

CHIRIQUÍ: Boquete, 1200–1500 m, *Woodson & Schery 727* (MO). Finca Lerida to Boquete, 1300–1700 m, *Woodson et al. 1163* (MO, NY).

12. GIBSONIOTHAMNUS

Gibsoniothamnus L. O. Williams, Fieldiana, Bot. 32: 211. 1970. TYPE: *G. pithecobius* (Standley & Steyerm.) L. O. Wms. = *G. cornutus* (D. Sm.) A. Gentry.

Shrubs, epiphytic, ?hemiepiphytic, or free standing, stems often angled. glabrate to pubescent with iniseriate multicellular sometimes gland-tipped hairs,

sometimes tuberculate. *Leaves* opposite, sometimes unequal, simple, entire, often coriaceous, pinnately 3–4 nerved on each side, the nerves well spaced, arcuate; petioles mostly short, not forming stipular ridges. *Inflorescences* terminal cymose racemes or panicles, often condensed and fasciculate, sometimes reduced to a few flowers, the peduncles mostly elongate, bracteate. *Flowers* showy, the calyx brightly colored, merging into the pedicel, cupular, 5-dentate, the teeth sometimes ventrally conduplicate, the sinuses then appearing truncate and membranaceous; corolla tubular, 5-lobed, the lobes short, rotund, quincuncial, bearded within near the point of the stamen insertion; stamens 4 in 2 pairs, the filaments bearded at the point of insertion, the anthers basally divaricate, with a broad, differentiated connective, dehiscing longitudinally, situated below the corolla mouth; disc apparently wanting; ovary 2-locular, the placenta median, many ovulate, the style glabrous, the stigma a terminal annulus, not bilobate. *Fruit* a juicy or mucilaginous berry; seeds numerous, prismatic, minutely ciliate with a gelatinous slimy covering, the endosperm extremely scant or wanting; embryo straight, cylindrical, the appressed cotyledons forming about ½ its length.

Gibsoniothamnus is a genus of 3 or 4 species of southern Mexico and Central America. The flowers are showy, presumably hummingbird pollinated, and the fruit is a berry. The plants are epiphytic, perhaps hemiepiphytic, or free-standing shrubs. Although numerous collections have been made in recent years, species limits are poorly drawn and the following treatment is highly tentative. The only element described in the genus which is not accounted for below is *Gibsoniothamnus moldenkianus* (Stands.) L. O. Wms. from Mexico, known only from the type which has not been studied.

Two collections at MO from Costa Rica (Alajuela) with small leaves and small white flowers may represent still another species.

Family placement of this genus is uncertain, and it is here treated in the Scrophulariaceae mainly for editorial considerations. Species of *Gibsoniothamnus* have been described in the Verbenaceae, Scrophulariaceae, and Bignoniaceae, and routine herbarium determinations have frequently placed specimens in the Solanaceae, Gentianaceae, or Ericaceae. From the Verbenaceae it may be excluded by its many ovulate ovary, from Gentianaceae by its imbricate corolla and lack of endosperm, from Ericaceae by its 2-loculed ovary, and from the Solanaceae by its opposite leaves, lack of internal phloem and the orthodirectional placement of the ovary. *Gibsoniothamnus* is believed by Gentry (1971, 1974, and pers. comm.) and Williams (1970) to be closely related to *Schlegelia* Miq., another genus of uncertain placement. *Schlegelia* was treated in the Flora of Panama as a member of the Bignoniaceae and in Flora of Guatemala under the Scrophulariaceae. Leinfellner (1973) stated that the U-shaped placenta of the *Schlegelia* species he studied is more suggestive of the Scrophulariaceae than of the Bignoniaceae. Gentry's 1974 report that the ovary of *Gibsoniothamnus* is 2-locular to the top was verified by microtome sections, so this ovary differs conspicuously from the U-shaped placental situation of typical *Schegelia*. While this completely 2-locular ovary bespeaks a greater evolutionary distance between the two genera than assumed by earlier workers, it does not offer much guidance

as to the correct family placement of *Gibsoniothamnus*. Leinfellner (1972, 1973), Weber (1972), and Hartl (1956), who studied ovary structure in the Bignoniaceae, Gesneriaceae, and Scrophulariaceae, failed to report any characters which absolutely separate these families. Sunken peltate glands as in *Gibsoniothamnus* are more common in both Bignoniaceae and Gesneriaceae than in the Scrophulariaceae, and the entire leaves are uncommon but not unique in the Scrophulariaceae. The absence or extreme paucity of endosperm is more in harmony with the Bignoniaceae than either Scrophulariaceae or Gesneriaceae. Pubescence of the seeds is unusual in all three families although it does occur in the Gesneriaceae and a few Bignoniaceae, and the wings on typical seeds of the Bignoniaceae may derive from hairlike trichomes.

Literature:

Gentry, A. H. 1971. Note on *Gibsoniothamnus*. Fieldiana, Bot. 34: 55.
———. 1974. *Gibsoniothamnus* (Scrophulariaceae) in Panama. Ann. Missouri Bot. Gard. 61: 533–537.
Leinfellner, W. 1972–3. Das Gynözeum der Bignoniaceen. Österr. Bot. Z. 120: 269–277; 121: 13–22; 122: 59–73.
Weber, A. 1971. Zur Morphologie des Gynoeciums der Gesneriaceen. Österr. Bot. Z. 119: 234–305.
Williams, L. O. 1970. An overlooked genus of the Scrophulariaceae. Fieldiana, Bot. 32: 211–214.

a. Calyces, pedicels and stems copiously pilose with white or tawny hairs, 1–2 mm long; calyx more than 20 mm long ——— 3. *G. mirificus*
aa. Calyces, pedicels and stems glabrous or soon glabrescent; calyx less than 20 mm long.
b. Corolla white; flowers mostly solitary; calyx basally conspicuously cucullate, winged, or broadly deltoid, the teeth usually broad in fruit ——— 1. *G. alatus*
bb. Corolla pinkish to purplish; flowers mostly in subsessile fascicles; calyx basally flat, narrowly winged, or narrowly deltoid, the teeth usually apically narrow in fruit ——— 2. *G. cornutus*
c. Calyx sinuses truncate, calyces mostly less than 20 mm long ——— 2a. *G. cornutus* var. *cornutus*
cc. Calyx sinuses usually acute, calyces mostly more than 10 mm long ——— 2b. *G. cornutus* var. *latidentatus*

1. **Gibsoniothamnus alatus** A. Gentry, Ann. Missouri Bot. Gard. 64: 133. 1977 [1978]. TYPE: Panama, *Mori & Kallunki* 5449 (MO).

Shrub, ?hemiepiphytic or epiphytic, to 1.3 m tall; stems subterete or angled, slender, the nodes sometimes crowded. *Leaves* ovate, elliptical or obovate, apically obtuse or acuminate, basally narrowed, acuminate, the margins sometimes somewhat revolute, the major veins impressed above, slightly elevated beneath, mostly with 3 strongly ascending somewhat arcuate pinnate veins on each side of the costa, glabrate, sometimes with ciliate margined pores (domatia) in the vein axils beneath, sometimes minutely pubescent at the tip beneath, minutely glandular punctate beneath; petioles mostly drying dark, slightly channeled above, minutely pubescent beneath. *Inflorescences* reduced terminal racemes, few flowered, the flowers sometimes solitary, pedicels to 18 mm long,

slender but broadening upwards, glabrate, articulating at or just above the base, the bract deltoid, minute, often appressed to the pedicel. *Flowers* purple, the calyx ca. 1.8 mm long, the teeth ventrally conduplicate, the dorsal surface enated to form narrow wings which run from the base of the cup to the tips, the sinuses acute in flower, nonmembranaceous, running down to 6–8 mm from the calyx base, in fruit forming a membranous sleeve, the cup not distinct from the wings; corolla white, tubular, ca. 18 mm long, ca. 3 mm thick, the lobes rotund, short, with a short, spreading limb; stamens not seen; style (Gentry) 18 mm long, the ovary globose. *Fruit* mostly enveloped by the calyx sleeve, the tip perhaps exserted.

This species ranges from Bocas del Toro to Darien, occurring from 300 m to perhaps 2,000 m. The four collections seen are far from homogeneous, the type and *Duke 15657*, both from Darien, have relatively large leaves to 8 cm long with well defined acuminate tips, whereas the other three more westerly collections have leaves not exceeding 3.5 cm, with blunt and scarcely acuminate tips. It is possible that these western collections represent a different species.

Gibsoniothamnus alatus is distinct in its calyx, the teeth of which form winging enations from the base of the calyx cup to the tips of the teeth. In fruit, there is also a well defined membranaceous sleeve truncating the calyx cup and running continuously and discretely abaxially to the teeth. This species is also distinct in its flower color which is reportedly a purple calyx with a white corolla. Mori & Kallunki note the fruit is pink.

COSTA RICA: Prov. Alajuela. Road between Cañas and Upala 8 km N of Bijagua, 300 m, *Croat 36050* (MO). 8 km N of Rio Naranjo on Cañas-Upala road, 400–500 m, *Utley & Utley 3161* (MO). PANAMÁ: BOCAS DEL TORO: Chiriquí Trail cloud forest between Quebrada Higueron and Gutierrez, *Kirkbride & Duke 754* (MO). CHIRIQUÍ: Cerro Colorado, road to copper mine 33.1 km beyond bridge over Río San Félix, 13.1 km beyond turnoff to Escopeta, 1400 m, *Croat 37200* (MO). DARIÉN: Elfin forest, Cerro Campamento, S of Cerro Pirre, *Duke 15657* (MO). N slopes of Cerro Pirre, *Mori & Kallunki 5449* (MO).

2. **Gibsoniothamnus cornutus** (Donnell Smith) A. Gentry, Fieldiana, Bot. 34: 55. 1971.

Schlegelia cornuta Donnell Smith, Bot. Gaz. (Crawfordsville) 16: 6. 1893. TYPE: Guatemala, *Heyde & Lux* ex pl. cit. *3004* (F, not seen; photo MO).
Clerodendron epiphyticum Standley, Publ. Field Mus. Nat. Hist., Bot. Ser. 22: 168. 1940. TYPE: Costa Rica, *Lankester 1296* (F, not seen; photo MO).
C. pithecobius Standley & Steyerm., Publ. Field Mus. Nat. Hist., Bot. Ser. 22: 373. 1940. TYPE: Guatemala, *Standley 67887* (F, not seen).
C. mimicum Standley & Steyerm., Fieldiana, Bot. 23: 227. 1947. TYPE: Guatemala, *Steyermark 43267* (F, not seen).
Gibsoniothamnus mimicus (Standley & Steyerm.) L. O. Williams, Fieldiana, Bot. 32: 214. 1970.
G. pithecobius (Standley & Steyerm.) L. O. Williams, Fieldiana, Bot. 32: 214. 1970.
G. epiphyticus (Standley) L. O. Williams, Fieldiana, Bot. 34: 120. 1972.
G. allenii A. Gentry, Ann. Missouri Bot. Gard. 61: 534. 1974 [1975]. TYPE: Panama, *Gentry 758* (MO).
G. pterocalyx A. Gentry, Ann. Missouri Bot. Gard. 61: 535. 1974 [1975]. TYPE: Panama, *Kirkbride & Duke 1020* (MO).

2a. **Gibsoniothamnus cornutus** (Donnell Smith) A. Gentry var. **cornutus**.

Shrub, ?hemiepiphytic or epiphytic; twigs strongly angled or winged, glabrous;

stems strongly 2–4 angled or sharply narrow winged at the nodes, angled into the petioles, the internodes mostly short; bark drying gray. *Leaves* opposite, simple, entire, obovate, 3–9 cm long, 12–25 mm wide, apically indistinctly short acuminate or obtuse, basally obtuse or acute, mostly drying slightly revolute, slatey above, ochraceous beneath, the major venation impressed above, elevated and contrasting beneath, the usually 3 pinnate veins on each side arcuate and ascending, the proximal pair near the margin and often giving the leaf a plinerved appearance, minor venation obscure, ciliate at least apically and along the costa beneath, glabrescent or sparingly pubescent at maturity, some populations barbulate and pitted in the vein axils beneath, minutely punctate on both sides with submerged peltate trichomes; petiole 7–14 mm long, channeled above, glabrate or sparingly hispid. *Inflorescence* terminal, cymose, congested, sometimes subumbellate and many flowered; peduncle short to obsolete, strongly angled; pedicels glabrate to 3.5 cm long, subtended by small bracts, flat and deltoid or linear and to 6 mm long, pubescent with nearly straight white tuberculate hairs. *Flowers* showy, the pedicels, the calyx and the corolla magenta; calyx merging with the apically expanded pedicel, cupular or campanulate, 2–5 mm long (excluding teeth), somewhat succulent, the 5 triangular costa conspicuous or not, running into the teeth, the teeth deltoid to subulate, 3–5 mm long, becoming 6–9 mm long in fruit, sometimes laterally compressed and appearing cucullate, glabrate or sparingly pilose with gland tipped hairs, the sinuses obtuse, rounded or truncate, sometimes thin, especially in fruit; corolla tubular, to 3 cm long, 3 mm wide, sometimes slightly curved, the 5 short, rotund lobes quincuncial in bud, thinning at the margins, ciliolate, the throat pulverulent, the tube bearded just below the point of the stamen insertion; stamens 4, the filaments densely bearded at the point of insertion, narrowed at the tip, glabrous, the anthers situated in 2 proximal pairs just below the corolla mouth, 2-locular, the locules proximal, dehiscing longitudinally, the connective differentiated, somewhat discolorous; ovary obovoid, apically flat or depressed, glabrous, the stigma flat, terminally annular, slightly broader than the style. *Fruit* a berry, nearly included in the calyx cup, 2-locular, many-seeded; seeds numerous, 3–4 mm long, wedge shaped with 1 end acute, strongly angled, minutely pubescent, mucilaginous and slimy.

This species ranges from Guatemala to Panama, and the typical variety has a calyx with truncate sinuses and somewhat enated or winging costas. The flowers are reported as purplish. The type collection of *G. pterocalyx* has slightly different leaf texture from other collections seen.

CHIRIQUÍ: Between Pinola and Quebrada Seco on Chiriquicito-Caldera Trail, *Kirkbride & Duke 1020* (MO). COCLÉ: El Valle de Antón, 1000 m, *Allen 1824, 2385, 3414* (all MO). Cerro Pajita, N of El Valle de Antón, 3500 ft, *Allen 4496* (MO). Cerro Pilón, to 2900 ft, *Dwyer 8676* (MO). Cerro Pilón near El Valle, *Duke 12149, 13189* (both MO). Top of Cerro Pilón, *Gentry 758* (MO, NY). Trail from La Mesa towards los llanos, *Luteyn 4110* (DUKE). Trail to La Mesa ca. 4.5 mi beyond El Valle de Antón, *Wilbur & Luteyn 11670* (DUKE). DARIÉN: Upper Tyler Kittredge gold mining camp, headwaters of Río Tuquesa, *Croat 27281* (MO).

2b. **Gibsoniothamnus cornutus** var. **latidentatus** (A. Gentry) D'Arcy, comb. nov.—FIG. 11.

G. latidentatus A. Gentry, Ann. Missouri Bot. Gard. 61: 536. 1974 [1975]. TYPE: Panama, *Gentry 759* (MO).

Shrub resembling the typical variety. *Leaves* glabrate and lacking domatia or barbulate vein axils beneath. *Flowers* with the calyx teeth basally broad and connate, tangentially flattened, the sinuses acute, nonmembranaceous.

This variety is much like the typical variety but differs in lacking domatia on the leaf undersides and in the form of the calyx. In addition to having basally broad, flat teeth, the calyx remains succulent in fruit. It is known only from Cerro Jefe in Central Panama, 500–950 m elevation.

PANAMÁ: Camino de Llano a Cartí, *Correa et al. 1888* (MO). Cerro Jefe, *Croat 17343* (MO). El Llano-Cartí Road, 7–12 km from Interamerican Highway, *Croat 25138* (MO). Cerro Jefe, *D'Arcy 11385* (K, MO, PMA, US); *Dressler 3448* (MO); *Duke 8175* (MO); *Dwyer et al. 7293* (MO); *Dwyer & Gauger 7351* (MO); *Gentry 759* (MO). El Llano-Cartí Road, 340 m, *Gentry 1181* (DUKE, MO), *1321* (MO); *Gentry & Mori 14203* (MO, PMA), *14216* (MO). Cerro Jefe, *Kirkbride & Crebbs 27* (MO); *Luteyn 3201* (DUKE). Cerro Campana, *Luteyn & Kennedy 1789* (DUKE). Cerro Jefe, *Luteyn & Kennedy 3947* (DUKE). El Llano-Cartí Road, *Mori & Kallunki 5104* (MO). 5–10 km NE of Altos de Pacora, 700–800 m, *Mori & Kallunki 6064* (MO). Cerro Jefe, *Mori & Kallunki 6076* (MO). El Llano-Cartí Road, *Nee & Tyson 10991* (MO). Cerro Jefe, *Skog et al. 4220* (MO); *Tyson 3529* (DUKE). VERAGUAS: Descent to Río Caloveborita ca. 16 km NW of Santa Fé, 650 m, *Dressler 5142* (MO). Shoulder of Cerro Tuti, *Folsom & Edwards 3345* (MO).

3. **Gibsoniothamnus mirificus** A. Gentry, Ann. Missouri Bot. Gard. 64: 133. 1977 [1978]. TYPE: Panama, *Croat 34298* (MO, holotype; PMA, isotype).

Epiphytic *shrub*, the twigs stout, angled, drying yellow, hispid pilose with stout, curved or straight tawny many-celled hairs on scarcely elevated, many-celled bases, branches gray, scabridulous but soon glabrescent and becoming subterete. *Leaves* ovate, elliptical or obovate, often broadly so, apically short acuminate, blunt, basally obtuse or rounded, to 8 cm long, 4 cm wide, the veins impressed above, elevated and contrasting beneath, ca. 3 pinnate veins on each side, strongly ascending and arcuate, the basal pair close to the margin, the loop connected near the margin, some short intermediate veins sometimes present, pilose with long, weak, slender, multicellular hairs overall, sometimes glabrescent except beneath on the major veins, inconspicuously glandular punctate above, more noticeably so beneath; petiole 7–9 mm long, flat or slightly channeled above, hispid pilose with tawny hairs, pinkish (Whieler), usually drying dark. *Inflorescence* terminal, fasciculate or umbellate, sometimes reduced to a solitary flower, the peduncles 3–5 mm long, glabrous or pubescent, persistent, subtended by minute linear to deltoid pubescent bracts; pedicels reddish (Whieler), articulating at the base, 10–15 mm long, slender but broadening upwards, hispid pilose with tawny hairs 1–2 mm long. *Flower* with the calyx merging into the pedicel, pinkish, ca. 3 cm long (including teeth), the teeth narrowly deltoid, ca. 2 mm wide at the base, 2.0–2.5 cm long, continuous with the ribs of the cup, the sinuses obtuse or acute, much broader and subtruncate in fruit, pilose overall with weak whitish hairs 2–3 mm long; corolla tubular, red or pink, 3–4 cm long, slightly curved and slightly contracted in the upper half, the lobes short, rotund, 3 mm long, subequal but forming a definite lip, ciliate but otherwise glabrous outside; androecium and gynoecium not examined. *Fruit* not seen.

B
C
A

Gibsoniothamnus mirificus is distinct from other members of the genus in its overall hairiness and in its long slender calyx teeth which extend over ½ the length of the corolla. It is known from Santa Rita Ridge just southeast of Colon, and from the Continental Divide near El Cope in Cocle Province.

COCLÉ: Lumber camp 7 km N of El Copé, 900 m, *Folsom 1286* (MO). COLON: Santa Rita Ridge road, 380 m, *Croat 34298* (MO); *Folsom 3705* (MO); (grown to maturity and pressed in cultivation), *Whieler 77103* (MO).

13. LAMOUROUXIA

Lamourouxia H.B.K., Nov. Gen. Sp. Pl. 2, ed. folio 269; ed. quarto 335. 1817 [1818]. nomen cons. vs. *Lamourouxia* C.A. Agardh. 1817. (Algae).

LECTOTYPE: *L. multifida* H.B.K.,[8] type cons.

Erect perennial *herbs* or slender *shrubs*; roots fibrous or arising from a stout caudex, perhaps parasitic on other plants. *Leaves* opposite, often reduced upwards, dentate, serrate or narrowly pinnatisect and appearing compound, mostly pubescent with simple, glandular or branched hairs, sometimes scabrous, short petiolate or sessile. *Inflorescences* terminal racemes, the pedicels short, subtended by foliose bracts. *Flowers* with the calyx cupular or campanulate, 10-nerved, 4(5) lobed to about ½ way down, the lobes obtuse, deltoid or linear; corolla showy red, orange, yellow or white, tubular, tomentose outside, and sometimes within, 2-lipped, the lobes short, mostly recurved; stamens 4 or 2 and 2 staminodes, the filaments inserted low on the tube, the lower (dorsal) anthers situated against the upper corolla lip, barely exserted, the upper two anthers situated lower in the tube against the lower side, sometimes reduced to tufts of hairs, the anthers U-shaped, sometimes auriculate or pointed, mostly pilose; ovary 2-locular, narrow, the style slender, the stigma punctiform. *Capsule* ovoid or elliptical, exserted from the calyx which tardily ruptures, loculicidally dehiscent, the valves sometimes beaked; seeds numerous, ellipsoidal or oblong, the testa light colored, honeycomblike.

Lamourouxia is a genus of about 26 species ranging from Mexico to Peru. The plants are usually recognizable by their slender, often wandlike stems with numerous small leaves, and tubular, pubescent, red or orange flowers. Ernst (1972) divided the genus into three sections based primarily on the degree of reduction of the upper (shorter) pair of stamens. The two Panamanian species are members of sect. *Hemispadon* which has only two fully developed anthers, the other two rudimentary. *Lamourouxia lanceolata* Benth., also of sect. *Hemi-*

[8] For discussion of lectotypification of this genus see Taxon 18: 479. 1969. The International Code of Botanical Nomenclature 1972 incorrectly noted *L. virgata* Kunth as the type species.

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FIGURE 11. *Gibsoniothamnus cornutus* var. *latidentatus* (A. Gentry) Kuntze.—A. Habit (×¾).—B. Embryo (×34½).—C. Seed (×34½) note fine radial pubescence and fine hairs from the end. The pubescence supports a mucilaginous covering. [After *Mori-Kallunki 6149* (MO).]

spadon which has only two fully developed anthers, the other two rudimentary. *Lamourouxia lanceolata* Benth., also of sect. *Hemispadon*, occurs from Costa Rica to Mexico and may be expected in Panama. *Lamourouxia lanceolata* differs from the two species now known from Panama in having narrow leaves which are glabrous above and calyces which are glabrous to scurfy pulverulent with indiscernible hairs. *Lamourouxia virgata* H.B.K. occurs in the mountains of Colombia but does not reach Panama or Central America. It is a member of sect. *Adelphidion* which has reduced but still functional upper (ventral) anthers situated against the lower side of the corolla.

Literature:

Ernst, W. R. 1972. Floral morphology and systematics of *Lamourouxia* (Scrophulariaceae: Rhinanthoideae). Smithsonian Contr. Bot. 6: 1–63.

a. Leaves scabrous above, basally obtuse; calyx mostly lacking glandular hairs ---------- 1. *L. gutierrezii*

aa. Leaves softly pubescent above, basally truncate to auriculate; calyx with copious, glandular hairs ---------- 2. *L. viscosa*

1. **Lamourouxia gutierrezii** Oerst. in Benth. & Oerst., Vidensk Meddel Dansk Naturhist. Foren. Kjøbenhaun 1853: 29. TYPE: Costa Rica, *Oersted* 9398 (C, not seen).

L. scabra Benth. ex Seemann, Bot. Voy. Herald 177, *pl.* 33. 1854. SYNTYPES: Panama: *Seemann* (BM, not seen; photo MO); Boquete, *Seemann* (K, not seen).

Erect perennial *herbs* or *shrubs*, perhaps hemiparasitic on the roots of other plants, to 2 m tall, the stems slender, often woody below, drying dark, puberulent with short, weak, blackish, multicellular, rarely branched hairs; branching characterized by long wandlike stems and short lateral branches 5–15 cm long. *Leaves* opposite or verticillate, ovate, mostly 10–15 mm long, ca. 5 mm wide, elliptical or obovate, apically acute, basally cuneate, the margin dentate with ca. 5 rounded, callose and revolute margined teeth on each side, scabrous and shiny above, tomentose beneath with longer, stouter hairs on the veins, the venation pinnate with ca. 5 lateral veins on each side, impressed above, elevated beneath; petiole to 2 mm long, canaliculate, pilose beneath. *Inflorescences* terminal racemes, the flowers congested or well spaced; pedicels tomentose, ca. 5 mm long, subtended by a small foliaceous bract. *Flowers* with the calyx cupular, 7–9 mm long, 4-lobed, the lobes obtuse or deltoid, ca. 3 mm long, tomentulose outside, glabrate within, 10-nerved; corolla red or orange, 2.5–4 cm long, tubular, tomentulose outside with branched hairs, more so upwards, 2-lipped, the lips ca. 12 mm long, apically recurved, the upper lip glabrate within except at the apex, the lower lip long pilose in the upper ⅔, bearded at the level of stamen insertion, stamens 2, the filaments inserted low on the lower side of the tube, bearded at point of insertion, otherwise glabrous, the anthers connivent, positioned against the upper lip and barely exserted, U-shaped with pointed auricles, long pilose, 2-thecate, 3–4 mm long; staminodes 2, inserted low on the upper side, the

filaments slender, terminating in tufts of hair or rarely in rudimentary anthers, situated about ½ way up the corolla; ovary and the style glabrous, the stigma punctate, slightly immersed in stylar tissue. *Capsule* ovoid, black, ca. 10 mm long, 7–8 mm wide, loculicidally dehiscent, the valves short beaked; seeds stramineous, oblong, 1.5 mm long, pitted reticulate, numerous.

This species is known only from the uplands of Panama and Costa Rica. Its leaves are generally smaller and more numerous than those of the other Panamanian species, *L. viscosa*.

CHIRIQUÍ: Paso Ancho to Monte Lirio, upper valley of Río Chiriquí Viejo, 1500–2000 m, *Allen 1496* (MO, NY). W slopes of S flank of Cerro Horqueta, 1640 m, *Cochrane et al. 6255* (MO). El Barú above Boquete, 1200–1800 m, *D'Arcy 9233, 9935* (both MO). 3 km NE of El Hato del Volcán, 1800 m, *Davidse & D'Arcy 10414* (MO). Bajo Mono, 4500 ft, *Davidson 475* (MO). Valley of Río Chiriquí Viejo N of Volcán City, 5200–5600 ft, *Duke 9028* (MO, OS). From Boquete to 3 mi N, 3300–4200 ft, *Lewis et al. 398* (MO). Río Caldera beyond Bajo Mono ca. 4 mi NW of Boquete, 4200 ft, *Wilbur et al. 13526* (DUKE, MO, PMA). Bajo Quiel ca. 4 mi NW of Boquete, 1350 m, *Wilbur et al. 15506* (DUKE, MO, PMA). Río Caldera ca. 3 km beyond Bajo Mono, ca. 4 mi NW of Boquete, 1500 m, *Wilbur & Luteyn 19199* (DUKE).

2. **Lamourouxia viscosa** Kunth, Nov. Gen. 2, ed. folio 272. 1817. TYPE: Mexico, Humboldt & Bonpland (P-H.B.K. & P, fide Ernst 1972, neither seen).—FIG. 12.

Erect *herbs* or *shrubs* to 2(3) m tall; sometimes unbranched, the branches and stems slender, scurfy tomentulose with greyish indumentum, the hairs weak, blackish, several celled, sometimes branched; stems mostly terete. *Leaves* opposite, reduced in size upwards, sessile, ovate, apically obtuse, basally truncate to auriculate, the margins with numerous, sharp, sometimes callose teeth, mostly 2–4 cm long, 1–2 cm wide, somewhat coriaceous, both sides velutinous above with short whitish hairs, the venation obscure above, prominent beneath, the midvein and 2–4 strongly ascending lateral veins on each side conspicuously elevated. *Inflorescences* terminal racemes, at first congested, elongating with maturity, the pedicels tomentose, 3–4 mm long. *Flowers* with the calyx ca. 7 mm long, cupular, glandular tomentose, 10-ribbed, 4–5 lobed, the lobes deltoid, 2–3 mm long, sometimes somewhat acuminate; corolla red, tubular, 3–4 cm long, 5–7 mm wide, pulverulent tomentose with dark hairs, 2-lipped; stamens 2, the lower pair of anthers held against the upper lip, tomentose, the 2 staminodes reduced to tufts of hairs; stigma punctiform. *Capsule* ovoid, black, apiculate, ca. 2 cm long, ca. 8 mm wide; seeds oblong, ca. 1.5 mm long, with a stramineous, deeply reticulate testa.

This species is the most variable and widespread in the genus (Ernst, 1972), ranging from northern Mexico to central Panama. In Panama it occurs at slightly lower elevations than the other species, *L. gutierrezii*.

CHIRIQUÍ: El Barú above Boquete, 1200–1800 m, *D'Arcy 9915* (MO). 1.5 mi from Boquete on road to David, *Dwyer & Hayden 7630* (MO). COCLÉ: El Valle, 600–1000 m, *Allen 1154* (MO). Hills N of El Valle, 800 m, *Allen 2235* (MO, NY). VERAGUAS: Hueco de Calobré camino hacia La Yeguada, *Carrasquilla et al. 287* (MO). La Yeguada a orillas del Río San Juan, *Correa & Dressler 1970* (MO). Between Laguna La Yeguada and Calobré, *Luteyn 1473* (DUKE).

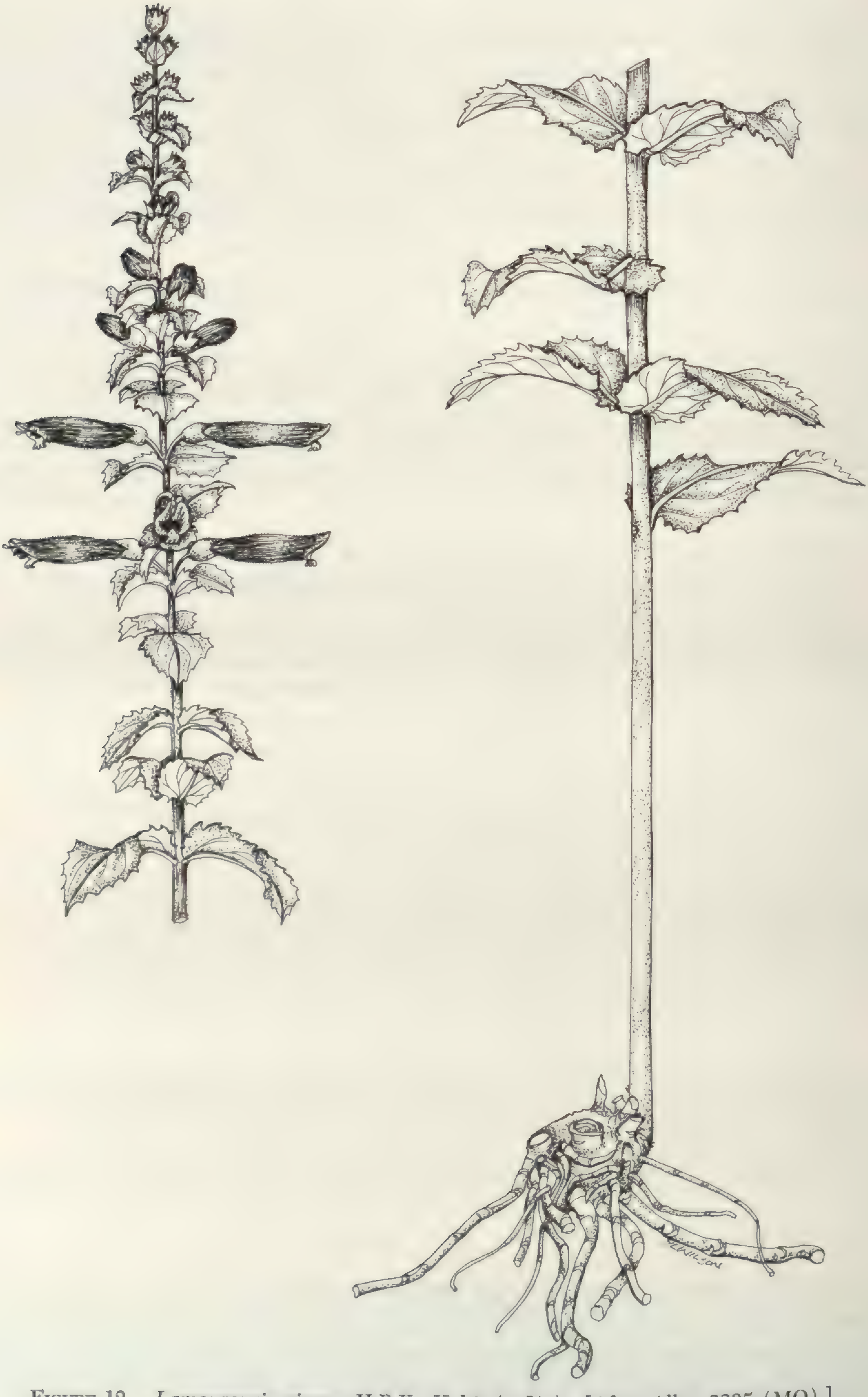

FIGURE 12. *Lamourouxia viscosa* H.B.K. Habit ($\times 7/10$). [After *Allen* 2235 (MO).]

14. LEUCOCARPUS

Leucocarpus D. Don in Sweet, Brit. Fl. Gard. 11, *tab. 124.* 1830. TYPE: *L. alatus* D. Don = *L. perfoliatus* (H.B.K.) Benth.

Robust *herbs*, glabrate, stems stout, strongly 4-angled or winged. *Leaves* opposite, lanceolate, denticulate, basally auriculate and appearing connate perfoliate, sessile but the basal part of the lamina contracted to appear petiolar. *Inflorescences* short pedunculate axillary cymes, the peduncle short, the flowers in several many-flowered clusters, the bracts small, narrow, subtending the pedicels and the inflorescence branches. *Flowers* with the calyx narrowly campanulate, 5-dentate, costate; corolla tubular campanulate, the 4 crenate lobes similar, glabrous outside, pubescent at the mouth within; stamens 4, alike, the 2 thecae basally divergent, staminode wanting; stigma 2-lamellate, situated just below the anthers. *Fruit* a white fleshy berry, 10 cm across, faintly bisulcate, the style persistent or leaving a beak; seeds numerous, minute, subglobose, reticulate.

Leucocarpus is a monotypic genus of mainland tropical America. It is distinctive in its robust stature, pedunculate cymose inflorescences, and baccate fruits.

1. **Leucocarpus perfoliatus** (H.B.K.) Benth. in DC., Prodr. 10: 335. 1846.—FIG. 13.

Mimulus perfoliatus H.B.K., Nov. Gen. Sp. Pl. 2: 371. 1817. TYPE: Colombia, *H. & B.*, not seen.
Conobea alata Graham, Edinburgh New Philos. J. 10: 168. 1830. TYPE: Cultivated, Scotland, not seen.
Leucocarpus alatus (Graham) D. Don in Sweet, Brit. Fl. Gard. II, 2; *tab. 124.* 1833.
Hemichaena fruticosa Benth., Pl. Hartw. 78. 1841. TYPE: Guatemala, *Hartweg 549* (?K, not seen).
Leucocarpus fruticosus (Benth.) Benth. in DC., Prodr. 10: 336. 1846.

Coarse, erect *herbs* or *shrubs* to 2.5 m tall, glabrate; stems stout, drying strongly angled, hollow, if puberulent soon glabrescent. *Leaves* opposite, appearing connate perfoliate but actually not so, lanceolate, to 20 cm long, ca. 3 cm wide, apically acute, basally narrowed and auriculate with an indistinct petiolar region, the margin serrate with numerous prominent but fine teeth, sometimes ciliolate, the midvein prominent, plane or impressed above, elevated beneath, lateral veins numerous, arcuate ascending, drying reticulate beneath, glabrate or with some short scattered hairs, copiously glandular dotted beneath on emerging; petiolar area broadly winged, mostly edentate. *Inflorescences* numerous short, several flowered contracted cymes to 4 cm long and 4 cm broad, the peduncles mostly 1–2 cm long, drying compressed, ciliolate, the bracts narrowly deltoid or lanceolate, costate, ca. 4 mm long, situated at the base of the pedicels and the peduncle branches. *Flowers* with the calyx 7–8 mm long, tubular campanulate, 5-lobed, the lobes 3–4 mm long, acute to linear, outcurving, extending downwards as prominent calyx costas, glabrous, the calyx tube enervate; corolla white, drying yellow, tubular to campanulate, ca. 1.5 mm long, glabrous outside or with minute glandular trichomes near the top of the tube, exserted ca. 10 mm from

FIGURE 13. *Leucocarpus perfoliatus* (H.B.K.) Benth.—A. Habit (×½).—B. Flower (×2). [After *Seibert 163* (MO).]

the calyx, 4-lobed, the lobes rotund, subentire, subequal, 3–4 mm long, the sinuses conspicuously infolded, the infolded portion densely bearded with white hairs; stamens 4, alike, the anthers free, alike, the 2 thecae divaricate and downcurved in a U over the filament apex, the filaments glabrous, slender, not apically expanded except as a pedicel-like connective; style shorter than the anthers, glabrous, terete; stigmas compressed, elliptical, apically acute, the ovary smooth, glabrous, eglandular, drying sulcate. *Fruit* a conspicuous, white, fleshy berry, ellipsoidal or ovoid, 10–18 mm long, septally sulcate, loosely enveloped by the slightly accrescent calyx until maturity, the calyx then dehiscing longitudinally to the base at one or more points, the style sometimes persistent, 4–5 mm long; seeds reddish brown, ca. 0.5 mm long, ellipsoidal, sometimes somewhat compressed, weakly pitted reticulate in indistinct longitudinal lines; placenta drying dark, massive, the septum drying light, indurate.

This species is a conspicuous element of natural disturbance at upper elevations in the Chiriqui Mountains. It ranges from Mexico (Jalisco) to Bolivia and Venezuela, but it is not known from the Antilles.

Leucocarpus perfoliatus blooms and fruits the year round.

BOCAS DEL TORO: Robalo Trail, N slope of Cerro Horqueta, 6000–7000 ft, *Allen 4806* (MO). CHIRIQUÍ: New Switzerland, valley of Río Chiriquí Viejo, 1800–2000 m, *Allen 1407* (MO, US). Cerro Punta, 7000 ft, *Blum et al. 2413* (MO, SCZ). Las Nubes, 5.5 km NW of Río Chiriquí Viejo W of Cerro Punta, 2000 m, *Busey 271* (MO). Camino entre Bambito y La Amenaza, 6000 ft, *Correa 1283* (MO). Hill above FSU cabin between Nueva Swissa and Cerro Punta, 1650 m, *Croat 26292* (MO). Las Nubes, 2000 m, *Croat 26421* (MO). Cerro Colorado copper mine development, 28 mi above San Félix, *Croat 33215* (MO). Bajo Chorro, Boquete District, 6000 ft, *Davidson 226* (MO). Road to Bajo Grande from Cerro Punta, *Folsom 4015* (MO). Slopes of Cerro Horqueta, 3500 ft, *Maurice 892* (US). Cerro Colorado, 50 km N of San Félix, 1200–1500 m, *Mori & Dressler 7880* (MO). Cerro Punta, 2½ km SW of town, *Mori & Kallunki 5663* (MO). Pastures around Boquete, 1000–1300 m, *Pittier 2914* (US). Cerro Punta, 6800 ft, *Ridgway & Solis 2406* (MO, SCZ). Monte Lirio, upper valley of upper Río Chiriquí Viejo, 1300–1900 m, *Seibert 163* (MO). Bambito, 1 mi SW of Cerro Punta, 5600 ft, *Tyson 5633* (MO, SCZ). Volcán, *Urriola 22* (MO). Thickets between Cerro Punta and Guadelupe, 1980 m, *Wilbur et al. 13040* (MO). Trail from Bajo Grande along Quebrada Grande to top of Paso de Respinga, 2100–2400 m, *Wilbur et al. 15128* (MO). Bajo Mona and Quebrada Chiquero, 1500 m, *Woodson & Schery 558* (MO).

15. LINDERNIA

Lindernia All., Mélanges Philos. Math. Soc. Roy. Turin 3: 178, *tab. 5, fig. 1.* 1766. TYPE: *L. pyxidaria* All. = *L. procumbens* (Krock.) Philc.

Vandellia P. Br. ex L., Syst. Nat., ed. 12, 2: 384, 422. 1767; Mant. Pl. 1: 89. 1767. TYPE: *V. diffusa* L. = *Lindernia diffusa* (L.) Dur. & Jacks.
?*Ilysanthes* Raf., Ann. Nat. 1: 13. 1820. TYPE: *I. riparia* Raf., based on *Lindernia attenuata* All.
Bonnaya Link & Otto, Icones Pl. Sel. 23. 1820. TYPE: *B. brachiata* Link & Otto.
Bazina Raf., Aut. Bot. 44. 1844. TYPE: *B. nudiflora* Raf., based on *Lindernia grandiflora* Nutt.
Pyxidaria Hall ex Kuntze, Rev. Gen. Pl. 2: 464. 1891. TYPE: *Lindernia pyxidaria* All.

Small paludal *herbs*, copiously branching, erect or ascending, sometimes rooting at the nodes, the roots fibrous, the stems mostly slender, drying angled, glabrate. *Leaves* opposite, small, entire or denticulate, sometimes punctate, 1–3-veined from near the base, basally cordate or truncate and clasping, or petiolate. *Inflorescences* of 1(–3?) flowers in the leaf axils, the pedicels slender,

drying angled, shorter or longer than the leaves, ebracteate. *Flowers* with the calyx 5-lobed, the lobes short or free to the base, costate and 1–3(–5) veined, the corolla prominently exserted from the calyx but sometimes cleistogamous and then the corolla little or not exceeding the calyx, campanulate, 2-lipped, the upper lip emarginate, the lower lip 3-denticulate, blue, white or purplish; stamens 4 or 2, the filaments inserted high on the corolla tube, the anthers connate in pairs, the thecae narrow, widely divergent and forming a cross, the filament sometimes conspicuously expanded just below the anther; ovary glabrous, eglandular, the style exserted or not, the stigmas compressed, ovate or discoid. *Capsule* elliptical or ovoid, sometimes slightly oblique, sometimes globose, dehiscing septicidally to the base, the placenta narrow, winged by the light colored septum; seeds numerous, mostly oblong, rarely curved, reticulate in transverse or longitudinal lines, these lines sometimes assuming the magnitude of small wings.

Lindernia is widespread in both temperate and tropical regions of the world, and some of the same species occurring in northern parts of the temperate zone, e.g., New Hampshire or Germany, also occur in lowland tropical Panama. The plants grow in wet, boggy areas, often in full sun. Some species are especially frequent weeds.

At one time, species with 2 anthers were separated from those with 4 anthers as the genus *Ilysanthes*, but several botanists have argued that this is not of generic importance. The distinctions of the South American sections were outlined by Miranda (1977). In addition to the three sections present in Panama, the New World hosts sect. *Bazina*, and the typical Old World section *Lindernia* has been doubtfully reported from the Guianas. Section *Bazina* is characterized by winged seeds (Pennell, 1935). Its sole species, *L. grandiflora*, has strongly angled, bent seeds, and the angles form only rudimentary wings. Two Panamanian collections, identified by asterisks under *L. anagallidea*, resemble the Florida species in overall leaf appearance and in having bent seeds with prominent angles. Thus the distinction of the Florida species and the section based on it is less than one might conclude from the literature.

Literature:

Miranda, D. O. 1977. Flavinoid and morphological studies of *Lindernia* Allioni (Scrophulariaceae) in South America. Bot. J. Linn. Soc. 75: 47–67.

Mukerjee, S. K. 1945. A revision of the Indo-Burmese species of *Lindernia* Allioni. Jour. Indian Bot. Soc. 24: 127–134.

Philcox, D. 1968. Revision of the Malesian species of *Lindernia* All. (Scrophulariaceae). Kew Bull. 22: 1–72.

a. Calyx lobed less than ½ way down; outline of placenta and septum broadly elliptical; leaves (bracts) subtending terminal flowers conspicuously reduced (sect. *Torenioides*) ---------- 2. *L. crustacea*

aa. Calyx lobed to near the base; outline of placenta and septum narrowly elliptical or conical; leaves (bracts) subtending flowers like the others (undifferentiated).

b. Flowers all subsessile, pedicels less than 2 mm long; leaves all shortly but distinctly petiolate; capsules often more than 5 mm long; leaves crenate dentate with numerous fine teeth (sect. *Numularia*) ---------- 3. *L. diffusa*

bb. Many or all flowers on distinct pedicels more than 2 mm long; upper (or all) leaves rounded or cordate clasping, the petioles obsolete; capsules less than 5 mm long; leaves entire or with few teeth (sect. *Brachycarpae*).
  c. Leaves mostly less than 8 mm long, all leaves rounded or cordate clasping; capsule mostly shorter or as long as the calyx ..... 1. *L. anagallidea*
  cc. Plants with many leaves more than 8 mm long; lower leaves narrowed and appearing petiolate; capsule mostly longer than the calyx ..... 4. *L. dubia*

1. **Lindernia anagallidea** (Michx.) Pennell, Acad. Nat. Sci. Philadelphia Monogr. 1: 152. 1935.

Gratiola inaequalis sensu auct., an Walt., Fl. Carol. 61. 1788. TYPE: not known.
G. anagallidea Michx., Fl. Bor. Amer. 1: 6. 1803. TYPE: Carolina, *Michaux* (P, not seen).
Lindernia dilatata anagallidea Muhl., Cat. Pl. Amer. Sept. 59. 1813. TYPE: ?Carolina, ?Pennsylvania, *Muhlenberg* (?PH, not seen).
Ilysanthes anagallidea (Michx.) Raf., Aut. Bot. 46. 1840.
I. inaequalis (Walt.) Pennell, Torreya 19: 149. 1919.

Delicate, paludal *herbs*, usually copiously branched, sometimes rooting at the nodes, prostrate or ascending, the branches slender, drying angled, glabrate. *Leaves* elliptic or ovate, sometimes rotund, mostly less than 8 mm long (Panama), pairs of leaves (bracts) subtending flowers often reduced, apically obtuse, sometimes acute, basally cordate or truncate and somewhat clasping, the margins usually thick, dentate or entire, the veins few, sometimes conspicuous, 1–3, palmate, glabrate; petioles wanting. *Inflorescences* solitary flowers in the leaf axils, the pedicels slender, drying angled, glabrate, exceeding the leaves, often greatly so, ebracteate. *Flowers* with the calyx 5-parted to the base, the lobes oblong, 3-nerved, apically acute, ca. 2.5 mm long, hardly accrescent. *Corolla* white, blue or mauve, ca. 7 mm long, campanulate; stamens 2, the filaments inserted ca. 3 mm from the base of the corolla, free ca. 1 mm, glabrous, compressed, the anthers connate, the thecae divaricate, narrow; style ca. 3 mm long, glabrous, apically short curved and flattened, the styles compressed, discoid. *Capsule* ellipsoidal, rotund, ca. 3 mm long, dehiscing septicidally, the placenta narrow, pitted, with narrow wings forming an elliptical outline; seeds numerous, yellow, ca. 0.5 mm long, reticulate laterally and longitudinally.

This diminutive species occurs from the northern United States south through the tropics into southern temperate areas. In Panama it occurs in wet weedy places at lower elevations.

Lindernia anagallidea is often difficult to separate from *L. dubia*. In Panama it is more delicate with smaller leaves, but in other countries, *L. anagallidea* is sometimes more robust.

For arguments in favor of the name used here and rejection of the name *L. inaequalis* see Pennell (1935).

CHIRIQUÍ: Marsh 12 km W of El Hato, *D'Arcy 10886* (MO). COCLÉ: In wet sand, valley floor and lower slopes along highway, El Valle, *Miller 1823* (US). In bogs, El Valle, 500–700 m, *Seibert 486* (MO). PANAMÁ: Sabana de Juan Corso near Chepo, 60–80 m, *Pittier 4743* (US). Near big swamp E of Río Tocumen, *Standley 26720* (US). In marsh, Juan Franco Race Track near Panama, *Standley 27826* (US). Near Matías Hernández, *Standley 28997* (US). Between Pacora and Chepo, *Woodson et al. 1646, 1648* (both MO).

2. **Lindernia crustacea** (L.) F. Muell., Syst. Census Austral. Pl. 1: 97. 1882.[9]

Capraria crustacea L., Mant. Pl. 87. 1767. LECTOTYPE: China (LINN 785.3, not seen) designated by Philcox, 1968.
Torenia crustacea (L.) Cham. & Schlecht., Linnaea 2: 570. 1827.
Pyxidaria crustacea (L.) Kuntze, Rev. Gen. Pl. 2: 464. 1891.

Prostrate or ascending paludal *herbs*, profusely branching, the stems drying angled, the angles ciliate, often purplish, slender, sometimes rooting at the nodes, the roots fibrous. *Leaves* opposite, rotund, apically obtuse or rounded, basally obtuse or truncate, crenate or serrate, to 15 mm across, punctate on both sides, glabrate above, beneath glabrate but sometimes pubescent on the veins; lower leaves distinctly petiolate, the petiole shorter than the leaves, thin winged, the costa pubescent beneath. *Inflorescence* a solitary flower in a leaf axil, or by suppression of the shoot, appearing terminal and 1–3 flowered, ebracteate, the pedicels slender, angled, ciliate, mostly exceeding the leaves, often purplish. *Flowers* with the calyx narrow, oblong or obconical, ca. 2 mm long, becoming 4 mm long in fruit, angled, glabrate or ciliate on the angles, with 5 subequal short lobes, the lobes often purplish; corolla blue or purple, exserted, ca. 4 mm long, 2-lipped, the upper lip longer, slightly 2-lobed or erose, the lower lip 3-lobed; stamens 4, didynamous, the upper pair inserted near the base of the corolla lip sinuses, the filaments glabrous, apically thickened, the thecae alike, divaricate and forming a nearly straight line, the lower pair inserted on the lower lip, the filaments slightly shorter, slenderer, not apically thickened, the thecae slightly unequal, the 2 anthers connivent, and the 4 thecae forming a cross; ovary glabrous, eglandular, the style slightly exceeding the anthers, the stigmas compressed, rotund discoid, papillose, drying elliptical. *Fruit* ovoid, included in the somewhat accrescent calyx, 4–5 mm long, the calyx costae prominent, the intercostal areas becoming hyaline, often splitting to the base, the style sometimes persistent, ca. 3 mm long; dehiscing septicidally to the base leaving the narrow pitted placenta winged by the thick, indurate, elliptical septum; seeds oblong, yellow, tuberculate in lines, ca. 0.5 mm long.

This weedy species is widely distributed in both New and Old Worlds.

BOCAS DEL TORO: Santa Catalina, *Blackwell et al. 2745* (DS). Almirante, *Blum 1323* (MO, SCZ). Railroad tracks near Milla 7.5, *Croat & Porter 16454* (MO). Railroad tracks near Milla 5, *Croat & Porter 16481* (MO). Changuinola, *D'Arcy 11162* (MO). Changuinola to 5 mi S at junction of Río Terebé, 100–200 ft, *Lewis et al. 788* (MO, US). Chiriquicito to 5 mi S along Río Guarumo, *Lewis et al. 1965* (MO, US). CANAL ZONE: Near mouth of Río Chagres, *Allen 894* (MO). Frijoles, *Croat 6269* (MO). Los Ríos, *Croat 11460* (MO). Between Frijoles and Monte Lirio, 30 m, *Killip 12119* (US). Pipeline Road ca. 16 mi N of Gamboa, *Lewis et al. 5441* (MO). Edge of lake near Madden Dam, *Mori & Kallunki 1991* (MO). 6 km E of Gamboa, *Nee 9036* (MO). Frijoles, *Standley 27409, 31495* (both US). 6 mi N of Gamboa near Río Frijol, *Tyson 1463* (MO, SCZ). Howard Air Force Base near Red Devil drop zone, *Tyson 1848* (SCZ). Miraflores Lake, *White 182* (MO). BARRO COLORADO ISLAND: *Croat 5991, 6579* (both MO); *Ebinger 545* (MO); *Foster 2290* (PMA); *Kenoyer 521* (US); *Shattuck 219* (MO); *Standley 40947* (US). CHIRIQUÍ: San Bartolo Arriba W of Puerto Armuelles, 125 m, *Croat 26729* (MO). Puerto Armuelles in bananas, *D'Arcy 10078*

[9] More synonyms are provided by Chamisso & Schlechtendal, Linnaea 2: 570–572. 1827, Philcox (1968), and Miranda (1977), but only the names presented here relate directly to the Panamanian flora.

(MO). David airport, 25 ft, *Lewis et al. 752* (MO). Quebrada Melliza 6 mi S of Puerto Armuelles, 0–150 m, *Liesner 455* (MO). San Bartolomé, Burica Peninsula, 0–50 m, *Woodson & Schery 924* (MO). COCLÉ: Boca del Toabré at confluence with Río Coclé del Norte, *Lewis et al. 5518, 5567* (both MO). COLÓN: From sea to top of ridge behind Garotte, *D'Arcy 9335* (MO). Mouth of Río Piedras, *Lewis et al. 3198* (DS). Portobelo, *Wilbur & Luteyn 11647* (DUKE). Roadside 5–7 mi SW of Portobelo towards Maria Chiquita, *Wilbur & Weaver 11206* (DUKE). DARIÉN: Boca de Cupe, 40 m, *Allen 901* (MO). Boca Quebrada Venado, Río Tuqueza, *Bristan 1097* (MO, OS). Road to Pinogana near El Real, *Croat & Porter 15476* (MO). Río Pirre, *Duke 4977* (MO, US). El Real, Rio Tuira, *Stern et al. 806* (MO). Río Sabana, *Tyson et al. 4780* (MO, SCZ). LOS SANTOS: Headwaters of Río Pedregal, 25 mi SW of Tonosí, 2500–3000 ft, *Lewis et al. 2940* (DS). PANAMÁ: Road to Cerro Azul 5 mi above Interamerican Highway, *Croat 11524* (MO). Top of ridge N of El Llano, *D'Arcy & D'Arcy 6047* (MO). 5–6 mi E of Chepo on Panamerican Highway, *Duke 4042* (MO). Agronomy School Farm, Tocumen, *Dwyer 4109* (US). Cerro Jefe, 1000 m, *Gentry 6754* (PMA). Sabana de Juan Corso, near Chepo, 60–80 m, *Pittier 4529* (US). SAN BLAS: Permé, *Cooper 219* (US). Puerto Obaldía, *Croat 1700A* (MO). Mandinga Airport, *Duke 14830* (OS). Outskirts of Puerto Obaldía, *Gentry 1577* (MO, SCZ). VERAGUAS: Mouth of Río Concepción, *Lewis et al. 2787* (MO).

3. **Lindernia diffusa** (L.) Wettst. in Engl. & Prantl. (editors), Natürlichen Pflanzenfamilien IV, 3b: 79. 1891.—FIG. 14.

Vandellia diffusa L., Mant. Pl. 1: 89. 1767. TYPE: Virgin Islands, *Brown* (?LINN 795–3). *Lindernia diffusa* (L.) Wettst. ex Durand & Jackson, Index Kewensis suppl. 1: 248. 1906. *Pyxidaria diffusa* (L.) Kuntze, Rev. Gen. Pl. 2: 464. 1891.

Paludal *herbs*, branching at the base or above, sometimes rooting at the nodes, the stems slender, angled, pilose in lines with weak, white hairs. *Leaves* opposite, rotund, ovate to rhombic, apically obtuse or rounded, basally cuneate to truncate, to 2 mm across, the margin crenulate, ciliate, minutely punctate, more noticeably so when young, glabrate or pubescent above, the veins somewhat pubescent beneath, the undersides sometimes purple, the midvein prominent with 2–3 lateral, ascending veins on each side; petiole winged, ca. 1 mm long. *Inflorescences* solitary or paired flowers in the leaf axils, the pedicel ebracteate, angled, broadening upwards indistinctly into the calyx, ca. 1 mm long. *Flowers* small, the calyx narrowly obconical, ca. 6 mm long, often pinkish or purplish, basally strongly angled, the angles ciliate, glabrous otherwise or pubescent, divided almost ½ way down into 5, narrowly acute, subequal lobes, sometimes tardily splitting to the base at the sinuses; corolla white and yellow, clavate in bud, ca. 8 mm long, glabrous outside, bearded within, 2-lipped, the upper lip emarginate, often purplish, the lower lip slightly shorter, 3-lobed; stamens 4, with 2 filaments inserted well below the top of the tube, glabrous, slender, broadening into a thick, deltoid connective, the anthers 2-thecate, the thecae divaricate in the lower ½, coherent in the upper ½, linear or ovate, yellowish, ca. 0.5 mm long, the lower 2 with the filaments inserted above the level of the 2 major sinuses, the free portion geniculate, glabrous, terete, ovary oblong, the style terete, ca. 3 mm long, the stigmas broadly ovate, somewhat reflexed, ca. 0.5 mm long. *Capsule* narrowly conical, sulcate, mostly prominently exserted from the calyx, to 9 mm long, scabridulous near the top, apiculate, greenish, sometimes septicidally dehiscent to the base, the placenta somewhat compressed, narrowly acute, the septum forming narrow hyaline wings; seeds yellowish or brownish, oblong, tuberculate, pitted in lines, angled, ca. 0.5 mm long.

FIGURE 14. *Lindernia diffusa* (L.) Wettst. Habit (×¾). [After *Croat* 6938 (MO).]

BOCAS DEL TORO: Changuinola Valley, *Dunlap* 386 (US). Changuinola to 5 mi S at junction of Ríos Changuinola and Terebe, 100–120 ft, *Lewis et al.* 921 (MO, US). Chiriquicito to 5 mi S along Río Guarumo, *Lewis et al.* 1968 (MO, US). Chiriquí Lagoon, *Wedel* 1157 (MO). Río Cricamola between Finca St. Louis and Konkintoë, *Woodson et al.* 1877 (MO). CANAL ZONE: Near mouth of Río Chagres, *Allen* 895 (MO). Barro Colorado Island, *Croat* 6938 (MO, SCZ), *11845* (MO). Frijoles, *Croat* 10372 (MO). Ft. Kobbe, *Duke* 3911 (MO). Chagres, *Fendler* 218 (MO). Pipeline Road, *Gentry & Dressler* 1984 (MO). Between Frijoles and Monte Lirio, *Killip* 12189 (US). Mount Hope Cemetery, *Standley* 28800 (US). Las Cruces Trail between Fort Clayton and Corozal, *Standley* 29041 (US). PANAMÁ: Bella Vista, *Standley* 25390 (US). Las Cascadas Plantation near Summit, *Standley* 29590 (US). Near Fort Sherman, *Standley* 31125 (US). COCLÉ: 12 mi NE of Penonomé, 1200 ft, *Lewis et al.* 1530 (DS). El Valle de Anton, 100–2000 ft, *Lewis et al.* 2502 (DS). 2 mi N of El Valle, 620–660 m, *McDaniel* 8293 (MO). COLÓN: Río Chagres 1 mi above Madden Lake, *Duke* 4484 (MO, DS). Confluence of Río Pacora and Río Corso, 450 m, *Duke* 11958 (MO, OS). Cerro Campana, *Lewis et al.* 3088, 4894 (both MO). Around Portobelo, *Pittier* 2442 (US). Near big swamp E of Río Tocumen, *Standley* 26592 (US). Between France Field and Catival, *Standley* 30380 (US). SAN BLAS: Mainland opposite Ailigandí, *Lewis et al.* 70 (MO). VERAGUAS: Mouth of Río Concepción, *Lewis et al.* 2798 (DS). Just S of Santa Fé, *Nee* 8075 (MO).

4. **Lindernia dubia** (L.) Pennell, Acad. Nat. Sci. Philadelphia Monogr. 1: 152. 1935.

Gratiola dubia L., Sp. Pl. 17. 1753. TYPE: Virginia, not seen.
Capraria gratioloides L., Syst. Veg., ed. 10. 1117. 1759. Based on *Gratiola dubia* L.

?*Ilysanthes riparia* Raf., Ann. Nat. 1: 13. 1820. TYPE: not seen. Perhaps based on *Lindernia attenuata* Muhl. cf. Aut. Bot. 45. 1840.
I. gratioloides (L.) Benth. in DC., Prodr. 10: 419. 1846.
I. dubia (L.) Barnhart, Bull. Torr. Bot. Club 26: 376. 1899.
Lindernia gratioloides (L.) Lloyd & Fouc., Fl. Ouest Fr. ed. 4. 246. 1886. (not seen, fide Pennell, Torreya 19: 149. 1919).

Paludal *herbs*, often branched, sometimes rooting at the nodes, the branches slender or stout, drying angled, glabrate. *Leaves* opposite, elliptical or ovate, to 30 mm long, apically rounded, obtuse or occasionally acute, the upper leaves rounded, truncate or cordate and clasping the stem, the lower leaves narrowed into a distinct, petiole-like region, the margins entire or denticulate, the margins not thickened, glabrate, scarcely punctate, the veins ca. 3 from near the base, 1 or more lateral veins often inserted higher on the costa. *Inflorescence* solitary or paired flowers in the leaf axils, the pedicels variable in length, those near the apex much exceeding the leaves, those near the base of the stems much shorter than the leaves, slender, drying angled, glabrate, thickening near the flower. *Flowers* with the calyx divided nearly to the base, the lobes subequal, oblong, acute, ca. 3 mm long, corolla white with a blue or purplish throat, 5–10 mm long, sometimes cleistogamous and hardly exceeding the calyx lobes; stamens 2, inserted in the throat, the anther thecae divaricate, narrow, connate; style slender, ca. 3 mm long, the stigmas compressed, rotund. *Capsule* about equaling the calyx lobes, broadly ellipsoidal, ca. 4 mm long, dehiscing septicidally.

This species is closely related to *L. anagallidea*, and the scant Panamanian material at hand is extremely difficult to separate from that species. In North America, plants are more robust and the characters noted in the key are much more apparent. This species occurs in the eastern United States and in Central America.

CANAL ZONE: Old Las Cruces Trail between Fort Clayton and Corozal, *Standley 29056*, *29225a* (both US).

16. MECARDONIA

Mecardonia Ruiz & Pavón, Fl. Peruv. & Chil. Prodr. 95. 1794; Syst. Veg. 164. 1798. TYPE: *M. ovata* R. & P.

Pagesia Raf., Fl. Ludov. 48. 1817. TYPE: *P. leucantha* Raf. = *Mecardonia acuminata* (Walt.) Small.

Erect or creeping *herbs*, annual or perennial, much branched, mostly glabrous, sometimes blackening on drying, gland dotted, stems angled. *Leaves* opposite, mostly serrate, basally narrowed, the costa prominent; petiole indistinct. *Inflorescence* solitary axillary flowers, the pedicels elongate, subtended by 2 basal bracts, the bracts often leaflike. *Flowers* yellow or white, the calyx 5-lobed, mostly to the base, the lobes often equal in length, quite unequal in width, the outer sepals much wider; corolla yellow or white, campanulate and somewhat bilabiate, glabrous outside, bearded at the mouth within; stamens 4, didynamous, inserted on the corolla throat, the anthers with the 2 thecae held apart on short arms; stigma 2-lobed, lamelliform, the ovary 2-locular, many ovulate. *Seeds* numerous, oblong, reticulate.

Mecardonia is a New World genus. North of Colombia it includes two well-marked species, while south of the Amazon there may be other species. It may be recognized by its gland-dotted foliage, by the pedicels basally bibracteate, and by the anthers separated by an armlike connective.

1. **Mecardonia procumbens**[10] (Miller) Small, Fl. S.E. U.S. 1065, 1338. 1903. —FIG. 15.

Erinus procumbens Miller, Gard. Dict. ed. 8. 1768. TYPE: ?Mexico, *Houston* (?BM, not seen).
Lindernia dianthera Swartz, Prodr. Veg. Ind. Occ. 92. 1788. TYPE: Hispaniola, *Swartz* (not seen).
Herpestis caprarioides H.B.K., Nov. Gen. Sp. Pl. 2: 368. 1818. TYPE: Colombia, *Humboldt* (B. Willd. *11541*, not seen, microfiche MO).
H. chamaedryoides H.B.K., Nov. Gen. Sp. Pl. 2: 369. 1818. nomen illegit. cites *Lindernia dianthera* Sw. TYPE: Ecuador (B. Willd. *11540*, not seen, microfiche MO).
H. colubrina H.B.K., Nov. Gen. Sp. Pl. 2: 368. 1818. TYPE: Peru, *Humboldt* (B. Willd. 11545, not seen, microfiche MO).
H. montevidensis Spreng., Syst. Veg. 2: 802. 1818. TYPE: Uruguay, *Sello* (not seen).
?*H. vandellioides* H.B.K., Nov. Gen. Sp. Pl. 2: 367. 1818. TYPE: Mexico (B. Willd. *11534*, not seen, microfiche, obscure, MO).
?*H. flagellaris* Cham. & Schlecht., Linnaea 2: 575. 1827. TYPE: Brasil (not seen).
H. peduncularis Benth., Bot. Mag. 2: 56. 1836. LECTOTYPE: Texas, *Drummond 75* (K, not seen).
H. chamaedryoides var. *peduncularis* (Benth.) A. Gray, Synop. Fl. N. Amer. 2: 280. 1878.
Monniera procumbens (Miller) Kuntze, Rev. Gen. Pl. 2: 463. 1891.
M. montevidensis (Spreng.) Kuntze, Rev. Gen. Pl. 3(2): 236. 1898.
M. procumbens δ *flagellaris* (Cham. & Schlecht.) Kuntze, Rev. Gen. Pl. 3(2): 236. 1898.
M. procumbens γ *montevidensis* (Spreng.) Kuntze, Rev. Gen. Pl. 3(2): 236. 1898.
M. chamaedryoides var. *peduncularis* (Benth.) Mohr, Contr. U.S. Natl. Herb. 6: 721. 1900.
M. dianthera (Sw.) Millsp., Field Mus. Nat. Hist., Bot. Ser. 2: 98. 1900.
Mecardonia peduncularis (Benth.) Small, Fl. S.E. U.S. 1065, 1338. 1903.
M. tenuis Small, Fl. S.E. U.S. 1065, 1338. 1903. TYPE: Florida, *Blodgett* (NY, not seen).
M. viridis Small, Fl. S.E. U.S. 1065, 1338. 1903. TYPE: Texas, *Heller 1460* (NY, not seen).
Bacopa procumbens (Miller) Greenm., Field Mus. Nat. Hist., Bot. Ser. 2: 261. 1907.
Herpestis procumbens Urb., Symb. Antil. 4: 558. 1911.
Bacopa chamaedryoides peduncularis (Benth.) M. C. Metz, Catholic Univ. Amer., Biol. Ser. 16: 173. 1934.
Pagesia dianthera (Sw.) Penn., Acad. Nat. Sci. Philadelphia Monogr. 1: 69. 1935.
P. peduncularis (Benth.) Penn., Acad. Nat. Sci. Philadelphia Monogr. 1: 65. 1935.
P. procumbens (Miller) Pennell, Acad. Nat. Sci. Philadelphia Monogr. 1: 68. 1935.
Bacopa procumbens var. *peduncularis* (Benth.) Fern., Rhodora 37: 442. 1935.
B. peduncularis (Benth.) Standl., Field Mus. Nat. Hist., Bot. Ser. 11: 174. 1936.
B. montevidensis (Spreng.) Hert. & Melch., Rev. Sudamer. Bot. 4: 191. 1937.
?*Pagesia vandellioides* (H.B.K.) Penn., Notul. Nat. Acad. Sci. Philadelphia 43: 2. 1940.
Mecardonia montevidensis (Spreng.) Penn., Proc. Acad. Nat. Sci. Philadelphia 98: 87. 1946.
?*M. vandellioides* (H.B.K.) Penn., Proc. Acad. Nat. Sci. Philadelphia 98: 87. 1946.

Creeping or ascending glabrous ephemeral *herbs*, mostly branching at the base, sometimes rooting at the lower nodes, the branches to 15 cm long, slender, flexuous; roots mostly short and fibrous, the stems sometimes strongly angled, sometimes with dark brown, multicellular, peltate glands. *Leaves* opposite, ovate, mostly 10–15 mm long, 8–10 mm wide, with about 7 even, ascending teeth on the upper ⅔ of the margin, apically obtuse, basally cuneate, mostly conspicuously (under a lens) glandular punctate with multicellular, sessile glands; petiole very short or indistinct. *Inflorescence* at first terminal, soon axillary, a solitary flower

[10] Other synonyms exist for this plant, but they do not relate directly to the Panama flora.

FIGURE 15. *Mecardonia* and *Bacopa*.—A–B. *Mecardonia procumbens* (Miller) Small.—A. Habit (×½).—B. Stamens (×7½). [After *Tyson 5356* (MO).]—C. *Bacopa salzmannii* (Benth.) Edwall. Stamens (×5). [After *Woodson et al. 1721* (MO).]

in a leaf axil, seldom geminate; pedicels slender, ca. 3 mm long, longer in fruit, bracts 2–4 mm long, linear, mostly entire, located at the base of the pedicel. *Flowers* ca. 8 mm long, the sepals free, the outer 3 sepals ovate, 7 mm long, 2–3 mm wide, larger in fruit, apically acute, basally obtuse or rounded, mostly lacking glands, inner 2 sepals linear, slightly shorter than the outer sepals; corolla tubular, exserted, yellow with purple lines, ca. 8 mm long, 5-lobed, the lobes recurved, rounded, sometimes irregularly crenulate, or emarginate, alike but the posterior pair with a short sinus, bearded in the throat; stamens 4, a rudimentary staminode sometimes present, the filaments glabrous, inserted at unequal heights in the lower ½ of the tube, free ca. 2 mm, the anther 2-thecate, the thecae oblong, held apart on expanded connectives, the connectives consisting of a discoid or ellipsoidal expansion at the filament apex and one slender arm to each theca; ovary narrowly ovoid, longitudinally sulcate, the styles 1.5 mm long, connate, apically

flattened, the stigma a linear crest on the slightly curved, flattened styles. *Capsule* narrowly ovoid, ca. 4 mm long, the walls stramineous, dehiscent loculicidally and septicidally from the apex; calyx accrescent, the outer sepals becoming 9 mm long and 5 mm wide; enlarged, linear placenta persistent on the withered capsule; seeds numerous, ovoid, 0.3 mm long, longitudinally ridged with a reddish brown reticulum.

BOCAS DEL TORO: Changuinola, 0–100 m, *D'Arcy 11153, 11179* (both MO). Runway at Almirante, *Lazor et al. 2319* (MO). Changuinola to 5 mi S at junction Río Terebé, *Lewis et al. 805A* (MO), *817, 1962* (both MO, US). Nievecita, 0–50 m, *Woodson et al. 1863* (MO, NY). CANAL ZONE: Chagres River near Juan Mina, *Bartlett & Lasser 16361* (MO). Colon to Empire, *Crawford 412, 583* (both PH). Pipeline Road 2½–5 mi from Gamboa gate, *Croat 9373, 33678* (both MO). Railroad track in front of Summit Garden, *D'Arcy 9303* (MO). Pipeline road to 18 km N of Gamboa, *D'Arcy 10636* (MO). Ft. Kobbe, *Duke 3954* (MO). Toro Point, Ft. Sherman, *Duke 4341* (MO). Madden Dam, *Ebinger 866* (MO, US). Chagres, *Fendler 213* (US). Road K-10 2 mi on Panamerican Highway toward Nuevo Emperador, *Lewis et al. 5218* (MO). Madden Forest, *Lewis et al. 5330* (DS, MO). Summit Gardens, *Mori & Kallunki 1891* (MO). SE side of Madden Lake near the Puente Natural, 90 m, *Nee & Hansen 14075* (MO). Railroad 3 mi W of Gamboa, *Nee & Mori 3609* (MO, PMA). Chiva-Chiva Trail, Red Tank to Pueblo Nuevo, *Piper 5736* (US). Sosa Hill, *Standley 26491* (PH, US). Near Fort Randolph, *Standley 28760* (US). Fort Sherman, *Standley 30986* (US). Chiva-Chiva Trail near Miraflores Lake, *Tyson 1382, 1387* (both MO). Gatún railroad station, *Tyson 3506* (MO). 5 mi N of Cocoli, *Tyson 3871* (MO). George Green Forest Preserve behind Cerro Tigre, *Tyson et al. 2508* (MO, PMA). Barro Colorado Island, *White 149* (MO). Miraflores Lake, *White 169* (MO), *266* (MO, PH). Pipeline Road N of Gamboa, *Wilbur & Weaver 11225* (DUKE). CHIRIQUÍ: Quebrada Tuco 9 mi S of Puerto Armuelles, *Croat 22093* (MO). Boquete, 3800 ft, *Davidson 575* (MO, US). Quebrada Melliza 6 mi S of Puerto Armuelles, *Liesner 486* (MO). Boquete, *Maxon 4965* (NY, US). COCLÉ: El Valle de Antón, 1000–?000 ft, *Lewis et al. 2604* (DS, MO). Above Penonomé, *Williams 528* (NY). COLÓN: Portobelo, *Wilbur & Luteyn 11651* (DUKE). DARIÉN: Boca de Cupe, ca. 40 m, *Allen 900* (MO). Airstrip at Caná gold mine, 480 m, *Croat 38011* (MO). Río Sambú upstream from Puerto Indio, *Dressler* (MO). Río Tuquesa at lower mining camp Charco Chiva, *Mori 6954* (MO). Caná, *Williams 734* (NY, US). HERRERA: 12.5 mi S of Ocú, 1200 ft, *Lewis et al. 1658* (MO, US). LOS SANTOS: 3 mi S of Carrete, ca. 5 mi S of Las Tablas, *Burch et al. 1245* (MO, US). Río Tonosí near Tonosí, *Lewis et al. 1574* (MO, US). Punta Mala, *Tyson 2706* (MO). PANAMÁ: Bayano Dam, *D'Arcy 9416* (MO). Without other locality, *Hayes 709, 823* (both NY). Punta Paitilla, *Heriberto 12b* (PH, US), *12* (US). Savanas N of Panama City, *Paul 621* (US). Near Matías Hernández, *Standley 28933* (US). Nuevo San Francisco, *Standley 30723* (US). Chepo, *Wilbur & Luteyn 11819* (DUKE). SAN BLAS: Puerto Obaldía, *Croat 17000* (MO). Soskatupu, *Duke 10187* (MO); *Elias 1667* (MO). Puerto Obaldía, *Gentry 1578* (MO).

17. MICRANTHEMUM

Micranthemum Michaux, Fl. Bor. Amer. 1: 10, *tab.* 2. 1803. nomen cons. TYPE: *M. orbiculatum* Michx. = *M. umbrosum* (Walt. ex Gmel.) Blake.—FIG. 16.

Globifera J. F. Gmelin, Syst. Nat. 2: 32. 1791. nomen rejic. TYPE: *G. umbrosa* Gmel., based on *"Anonymos" umbrosa* Walt.

[Anonymos Walt., Fl. Carol. 62. 1788. Name not intended as a generic name, cf. International Code of Botanical Nomenclature 1972 Article 20, note. TYPE: "A." umbrosa Walt.]

Diminutive creeping or floating *herbs*, glabrate, branching and rooting at the nodes. *Leaves* opposite, entire, mostly rotund, sometimes succulent; sessile or nearly so. *Inflorescences* solitary flowers in the leaf axils; pedicels short. *Flowers* minute, the calyx 4-parted to the base; corolla campanulate, 4-lobed, the lobes imbricate; stamens 2 inserted at the top of the corolla tube, the filaments genicu-

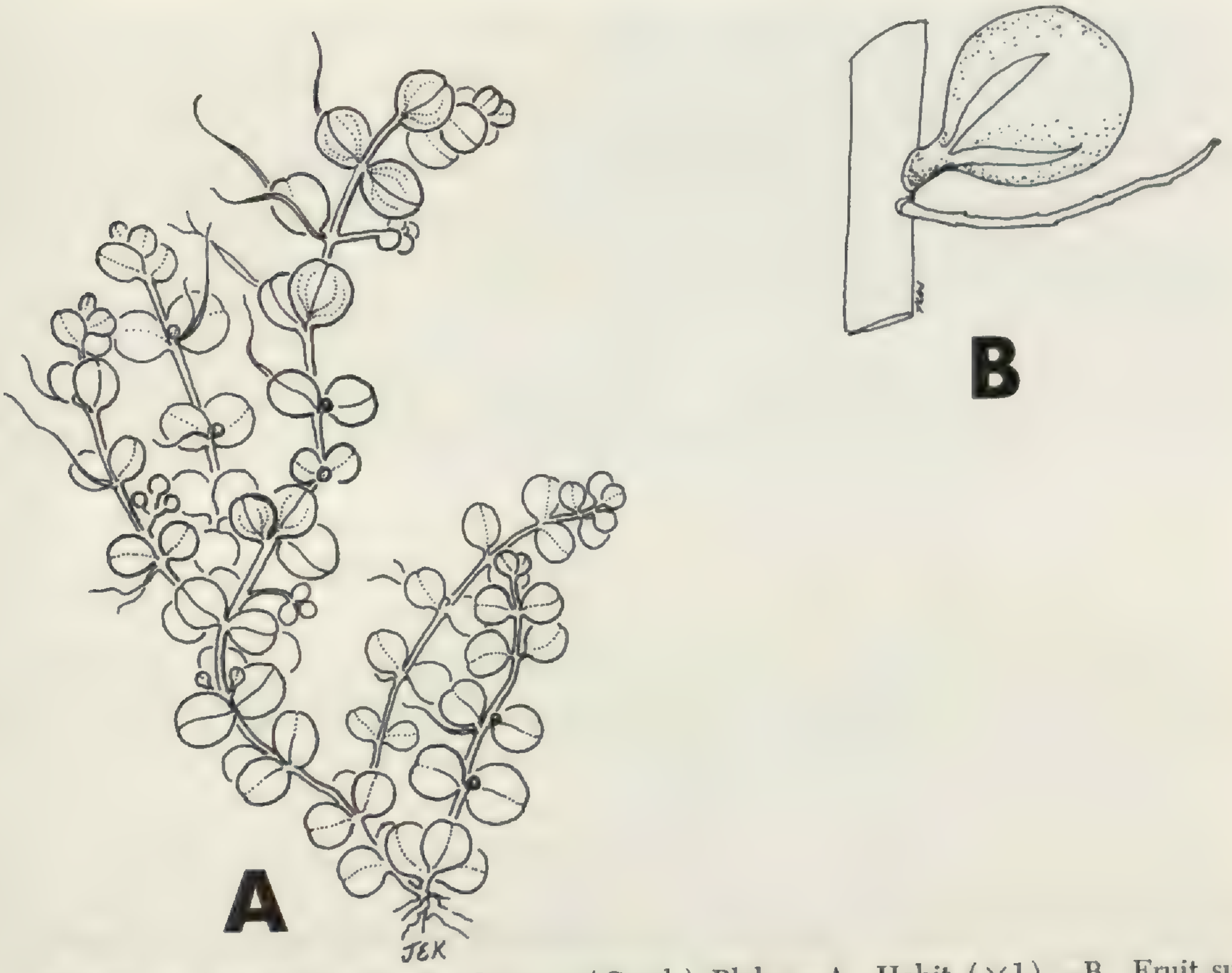

FIGURE 16. *Micranthemum umbrosum* (Gmel.) Blake.—A. Habit (×1).—B. Fruit subtended by adventitious root (×25). [After *McDaniel 8033* (MO).]

late, the 2 anther thecae separated by the slightly enlarged connective; style short, apically flattened and bent, the ovary globose, somewhat oblique, 2-locular, many ovulate. *Fruit* a slightly irregular, subglobose capsule, septicidally dehiscent, the septum remaining with the valves or evanescent; placenta ovoid, pitted; seeds yellowish, longitudinally ridged reticulate, numerous.

Micranthemum includes several species of temperate and tropical America. The type species, *M. umbrosum* (Walt. ex Gmelin) Blake, occurs in temperate eastern North America and in Brasil and Argentina. Several other species have been described from the New World tropics. The plants in this genus grow in moist shady habitats. Some botanists include *Hemianthus* Nutt. (1817) in *Micranthemum*. *Hemianthus* includes a number of superficially similar species which grow in the Antilles or in brackish ponds and flats in eastern North America. The type species of *Hemianthus*, *H. micranthemoides* Nutt., differs from *Micranthemum* in such important floral details as divided styles, elongate corolla tubes, fused calyx lobes, etc., which do not argue for unity of the two genera.

1. **Micranthemum pilosum** Ernst, Flora 57: 215. 1874. TYPE: Caracas, Venezuela, *Ernst* Nov. 1873 (B, if extant, not seen; photo US).

?*M. standleyi* L. O. Williams, Fieldiana, Bot. 34: 124. 1972. TYPE: Guatemala, *Standley 68810* (F, US, neither seen).

Diminutive floating or prostrate *herbs*; stems branching, glabrate, the nodes mostly shorter than the leaves; roots often arising from leaf- or flower-bearing nodes. *Leaves* opposite entire, orbiculate, ovate or elliptical, apically obtuse or rounded, basally cuneate obtuse; digitately 5-nerved, membranaceous or ?succulent; petioles mostly wanting. *Inflorescences* solitary flowers in the leaf axils; pedicels ca. 0.3 mm long, somewhat longer in fruit, broadening upwards. *Flower* 0.5–1.5 mm long, 4 parted to near the base, the lobes lanceolate, 0.5–1.0 mm long, pubescent; corolla 4-lobed, the lobes round, imbricate, exserted from the calyx; stamens 2, inserted at the top of the corolla tube, the filaments geniculate, curved, short, the thecae lenticular, separated by the somewhat enlarged and compressed connective; style short, included, apically compressed and curved, the stigma U-shaped; ovary subglobose, glabrous. *Fruit* a globose capsule ca. 1 mm across, chartaceous, septicidally dehiscent to the base, the placenta ovoid, pitted; seeds yellow, longitudinally reticulate, 0.3 mm long, oblong.

Micranthemum pilosum occurs on forest floors and in wet shady places in lowland Panama. It differs from *M. umbrosum* of the southeastern United States and parts of South America in its smaller flowers and fruits, and in the pubescent calyx which is shorter than the corolla.

Some plants from Texas and Louisiana now known as *M. umbrosum* also have these features and may be taxonomically distinct from plants of the eastern United States. The name *M. pilosum* is used with some hesitation as the photograph of the type does not reveal the floral details just noted. A study of *Micranthemum* material from the vicinity of Caracas is desirable.

CANAL ZONE: Old Las Cruces trail between Fort Clayton and Corozal, *Standley 29121* (PH, US). Fort Sherman, *Standley 30927* (PH). COCLÉ: Natá, *McDaniel & Tyson 14741* (MO). HERRERA: Cienaga Juncalillo near Correa, *McDaniel 8033* (MO). PANAMÁ: Río Pacora E of Panama City on Panamerican Highway, *Bartlett & Lasser 16961* (MO). Hills NE of Hacienda La Joya, *Dodge et al. 16923* (MO). Majecito, camino del Campo el Ranchon, *Rivera* 3 (PMA). Big swamp E of Río Tocumen, *Standley 26683* (US). Between Matías Hernández and Juan Díaz, *Standley 31949* (PH, US).

18. RUSSELIA

Russelia Jacq., Enum. Pl. Carib. 6. 1760. TYPE: *R. sarmentosa* Jacq.

Small, wiry *shrubs*, sometimes appearing herbaceous, the stems mostly ridged or angled, glabrate or pubescent. *Leaves* opposite or verticillate, membranaceous to coriaceous, ovate to lanceolate, sometimes reduced and caducous, entire, serrate or deeply incised, venation pinnate, sometimes glandular dotted; petioles present or wanting, mostly short; stipules wanting. *Inflorescences* axillary cymose clusters, mostly pedunculate; bracts foliaceous, reduced upwards on the flowering stems; bractlets narrow, sessile, mostly pubescent; pedicels slender. *Flowers* showy red or pink, rarely white; calyx 5-lobed to near the base, the lobes apically narrow, mostly with hyaline margins; corollas tubular, slightly bilabiate, the mouth mostly not spreading, mostly glabrous outside, mostly pubescent near the mouth and at the point of the stamen insertion within; stamens 4, didynamous, included, the filaments inserted just above the base of the tube, often pubescent

basally, the anthers ovoid, the cells divaricate, a short staminode mostly present; stigma entire, included, the ovary 2-locular, the ovules numerous on an expanded placenta. *Fruit* a rotund capsule, glabrous, septicidal, the style persistent or forming a beak, packed with long hairs derived from the placentas; seeds numerous, small, oblong, or elliptical, longitudinally striate or sometimes reticulate.

Russelia includes about 50 species, mostly Mexican, with one weedy species widespread in the neotropics and one species widely cultivated and escaping in the tropics. In Panama only the weedy *R. sarmentosa* and the cultivated *R. equisetiformis* are recorded. Species of this genus are usually easily recognized by the red or pink clusters of tubular flowers, glabrous outside, and by the angled stems.

Literature:

Carlson, M. C. 1957. Monograph of the genus *Russelia* (Scrophulariaceae). Fieldiana, Bot. 29: 231–292.

a. Plants nearly leafless; branches numerous and verticillate, slender; inflorescences 2-flowered; corolla glabrous inside; cultivated plant ..... 1. *R. equisetiformis*
aa. Plants with abundant ovate leaves; branches mostly opposite or ternate; inflorescences several-many flowered; corollas pubescent inside; common weed ..... 2. *R. sarmentosa*

1. **Russelia equisetiformis** Schlecht. & Cham., Linnaea 6: 377. 1831. TYPE: Mexico, *Schiede & Deppe 1187* (GH, not seen).

R. juncea Zucc., Flora 15 Beibl. 2: 99. 1832. TYPE: Cult. Munich, seed from Mexico, *Zuccarini* (?M, not seen).

Erect, branched, semileafless *herbs* to 1 m tall, the stems conspicuously 4–8 angled, the angles stramineous, glabrate, the branching often verticillate, each branch subtended by a leaf or adnate petiole. *Leaves* opposite or verticillate, subtending branches, oblong, elliptical or ovate, mostly less than 1 cm long, 6 mm wide, entire or serrate, the lateral veins 2–3 on each side, glabrate with a few scattered glands and minutely tomentose at the base of the costa above; petiole short, minutely tomentose above, the lower ½ tightly connivent with the axillary branch, medially callose and with thickened margins. *Inflorescences* paired, solitary or dichasial flowers scattered through the upper part of the plant, or condensed into open cymes or panicles, the peduncles to 15 mm long, the pedicels slender, sometimes purplish, 6–8 mm long, each subtended by a scalelike glabrate bract. *Flowers* small but showy, the calyx 2–3 mm long, the 5 deltoid lobes free to near the base, imbricate, glabrous, mostly eglandular; corolla tubular, scarlet, 15–30 mm long, glabrous but glandular in the throat, the lobes short, obtuse, similar; stamens 4, inserted at the base of the corolla tube, the anther thecae ovoid or elliptical, strongly divaricate, obliquely connivent at the base, 0.6–1.0 mm long, all situated on the lower side at the corolla mouth; style apically curved. *Capsule* not seen.

This species is perhaps native to Mexico but is widely cultivated and is now naturalized in many tropical and subtropical countries. In Panama it is known

only in cultivation but may be expected to persist from time to time. The broom-like, usually leafless stems and small showy red flowers are good features for recognition. Young plants, especially those grown in shelter from sun and wind, tend to have more leaves.

CANAL ZONE: Cultivated, Summit Gardens, *D'Arcy 10640A* (MO). PANAMÁ: Cultivated, Panama la Vieja, *Paul 782* (US).

2. **Russelia sarmentosa** Jacq., Enum. Pl. Carib. 6. 1760; Sel. Stirp. Amer. 178. 1763. TYPE: Cuba, *Jacquin*, not seen.—FIG. 17.

R. colombiana Pennell, Proc. Acad. Nat. Sci. Philadelphia 72: 186. 1920. TYPE: Colombia, *Smith 1361* (NY, holotype; isotype, MO).
R. flavoviridis Blake, Contr. U.S. Natl. Herb. 24: 22. 1922. TYPE: Guatemala, *Blake 7790* (US, not seen).
R. tabacensis Lundell, Contr. Univ. Michigan Herb. 6: 59. 1941. TYPE: Mexico, *Matuda 3524* (MICH).
R. oxyphylla Lundell, Contr. Univ. Michigan Herb. 7: 51. 1942. TYPE: Panama, *Bartlett & Lasser 16349* (MICH).

Erect, branching *herbs* to 2 m tall; stems conspicuously slender, stiff, glabrate, sometimes tufted at the nodes, 4–8 angled, the angles drying stramineous. *Leaves* opposite or ternate, ovate, mostly 2–4 cm long, 1.5–3 cm wide, apically obtuse, acute, or acuminate, basally rounded, obtuse or truncate, rarely cuneate, the margins sharply serrate to serrate crenate, the venation pinnate, with 3–5 conspicuous arcuate veins on each side, a minor vein extending to the tip of each tooth, ciliate, sparingly pubescent on each side with short, weak, whitish multicellular hairs, the hairs beneath fewer and confined mainly to the veins, scattered peltate glands abundant beneath and occasionally above; petioles short, 1–3 mm long, with thickened, basally tufted margins and with a medial callose thickening at the base. Inflorescences axillary fascicles of 1–3 short cymes; peduncles to 1.5 cm long, slender, angled, glandular, glabrate to pubescent, the nodes tufted and subtended with linear, pubescent bracts, the pedicels filiform, 1–3 mm long, slightly longer and stouter in fruit, sparingly glandular, glabrous, drying angled. *Flowers* small but showy, the calyx 5-lobed nearly to the base, ca. 4 mm long, the lobes long acuminate, basally broad and somewhat inflated to appear imbricate when pressed, glandular, the costa pubescent; corolla showy scarlet, tubular, 6–15 mm long, sparingly villous near the base, 4–5 lobed, the lobes mostly subequal, short, oblong, the lower lobe bearded near the throat within with stout, unicellular hairs, pilose near the point of filament insertion; stamens 4, the filaments inserted near the base of the corolla tube, glabrous, the anthers ellipsoidal, divaricate, the connective minute, the lower pair situated unequally about ⅔ way up the tube, the upper pair barely exserted; staminode short bearing a sterile knob; ovary smooth, glabrous, narrowly conical ellipsoidal, the stigma linear, situated near the lower anthers. *Capsule* globose turbinoid, ca. 4 mm across, dehiscing loculicidally and septicidally, the valves venose, beaked, not separating widely, the placentas dark, turbinoid, sometimes somewhat convoluted, the septum remaining with the valves, the locules filled with short, stout, tawny hairs arising from the placentas; seeds dark reddish brown, ca. 0.6 mm long,

FIGURE 17. *Russelia sarmentosa* Jacq.—A. Habit (×½).—B. Fruit (×3). [After *Allen 2770* (US).]

oblong, evenly pitted and reticulate, the pits with glandular material resembling that of the leaf undersides.

This species shows considerable variability, especially with respect to degree of pubescence and frequency of glands, but these differences do not warrant

taxonomic distinction. Carlson (1957) recognized several variants from Panama[11] but they represent unusual individuals rather than taxonomic populations.

Russelia sarmentosa is the most widespread species in the genus, ranging from Mexico to Colombia with representation in the Greater Antilles. It ranges from sea level to at least 1,500 m, occurring at forest edges, in pastures and along roadsides. It has considerable resistance to grazing. The erect, wiry stems and verticels of small, bright red flowers are distinctive.

CANAL ZONE: Between Cruces Trail and Madden Dam Road, *Bartlett & Lasser 16349* (MICH). Madden Forest, *Croat 8943* (DUKE, MO). Salamanca Hydrographic Station on gorge of Río Pequení, *Dodge et al. 16967* (MO). Drowned forest of Quebrada Tranquilla and branches, *Dodge & Allen 17324* (DS, MICH, MO). Balboa Heights, *Greenman & Greenman 5024* (MO). Cerro Ancón, *Heriberto 130* (US). Collin d'Ancón, Balboa, *Hladik 117* (MO). Ancón, *Paul 149* (US); *Piper 6021* (US). Río Grande near Culebra, *Pittier 2125* (US). Ancón Hill, *Standley 26325* (US). Sosa Hill, Balboa, *Standley 26478* (US). Balboa, *Standley 27000* (MO, US). Old Las Cruces Trail between Fort Clayton and Corozal, *Standley 29141* (US). Balboa, *Standley 29313* (US). Pueblo Nuevo, *White 297* (MO). CHIRIQUÍ: Paso Ancho to Monte Lirio, *Allen 1582* (MO, US). 5 mi S of Boquete, *Allen 4701* (MO). Ridge above Brazo Seco near Costa Rican Border, 100–200 m, *Croat 22552* (MO). 3 mi NE of El Hato del Volcán at base of Volcán Chiriquí, 1500–1800 m, *Davidse & D'Arcy 10363* (MO). Bajo Mono, Boquete District, 4700 ft, *Davidson 472* (MO, US). Lava fields near town of Volcán, 4600 ft, *Duke 9134, 9144* (both MO). Between Boquete and Cerro Horqueta, *Duke A13730* (DUKE, MO). Boquete, Llanos Francia, 4 mi toward Dolega, 4500 ft, *Dwyer & Hayden 7595* (MO). Llanos between Boquete and David, *Ebinger 748* (MO). Monchuila-Santo Domingo, *Gonzalez 30* (MO). 4.1 mi from Boquete on road to David, *Kirkbride 99* (MO). Boquete to 3 mi N, 3300–4200 ft, *Lewis et al. 358* (MO, US). 12.4 mi N of David, *Lewis et al. 708* (MO). 2.2 mi E of El Hato del Volcán, *Luteyn 808* (DUKE, MO). Between Cerro Vaca and Hato del Loro, 850–1100 m, *Pittier 5384* (US). Llanos Francia near Boquete, 3300 ft, *Stern et al. 1205* (MO). 3 mi N of El Volcán on old lava flow, 5000 ft, *Tyson 5724* (MO). Río Chiriquí Viejo valley, *White 77* (MO). 2 mi S of Puerto Armuelles, *Wilbur et al. 13587* (DUKE). COCLÉ: El Valle, 800–1000 m, *Allen 92, 1156* (both MO), *2770* (US). Between Cerro Pilón and El Valle de Antón, 700–900 m, *Duke & Dwyer 13907* (MO). W of Río Guias, *Gentry 5843* (MO). Ridge S of El Valle, 600 m, *Gentry 6795* (MO). Río Indio trail, El Valle de Antón, 500–700 m, *Hunter & Allen 335* (MO). 5 mi N of El Valle de Antón, *Luteyn 1182* (DUKE, MO). Crater around El Valle de Antón, *Luteyn 1259* (DUKE, MO). 2 mi N of El Valle, 620–660 m, *McDaniel 8259* (DUKE). Chigore de Penonomé, *Puga 4* (PMA). La Mesa, *Weaver & Foster 1656* (DUKE). W slopes of Cerro Pajita, headwaters of Río Guaybo, *Webster 16821* (MO). SE of El Valle de Antón, *Wilbur & Luteyn 11171* (DUKE). W slopes of Cerro Pajita in crater of El Valle de Antón, 650 m, *Wilbur et al. 15610* (DUKE, MO). Penonomé, 50–100 ft, *Williams 185* (US). COLÓN: Santa Rita Ridge 4–5.5 mi E of Transisthmian Highway, *Lewis et al. 5274* (DS, MO). DARIÉN: Chepigana, *Duke & Bristan 266* (MO, OS). HERRERA: Ocú, 100 m, *Allen 4047* (MO). 12.5 mi S of Ocú, 1200 ft, *Burch 1657* (MO). La Avena to Pesé, 22 ft, *Burch et al. 1298* (MO, US). Between El Potrero and Las Minas, *D'Arcy & Croat 4152* (MO). Between Las Minas and Pesé, *Duke 12342* (MO). 2½ mi N of Ocú, *Graham 227* (MICH). 10 mi S of Ocú, *Tyson et al. 2806* (MO). 1 mi N of Las Minas, *Wilbur 12072* (DUKE). PANAMÁ: Alcade Díaz, *Blandon 11* (PMA). Taboga Island, *Celestino 53* (US). Sabanas 3 mi E of Juan Díaz, *Cornman 2025* (US). Goofy Lake to Cerro Jefe, *Correa & Dressler 457* (DUKE, MO, PMA). 3 mi from Interamerican Highway on road to Cerro Campana, *Croat 12062* (MO). Cerro Campana, *Croat 12098* (MO). Near Calzada Larga, *Croat 12387* (MO). Cerro Jefe, *Croat 13041* (MO). Cerro Campana, *D'Arcy 9561* (MO). Río Chagres 1 mi above Madden Lake, *Duke 4458* (MO). Near top of Cerro Campana, *Duke 6004* (MO). Río Pasiga near first sharp bend above the sea, *Gentry 2249* (MO). Río Tocumen N of Chepo road, *Hunter & Allen 232* (MO). Cerro Azul, *Jaen 35* (MO). Cerro Campana on road to Su Lin, 650 m, *Kennedy et al. 2038* (MO). Taboga Island, 300 m, *Killip 3192* (US).

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[11] a. Stems glabrate.
b. Plants eglandular ..... *R. sarmentosa* fo. *eglandulata* Carlson
bb. Plants with glands ..... *R. sarmentosa* Jacq. fo. *sarmentosa*
aa. Stems pubescent ..... *R. sarmentosa* var. *nicaraguensis* Carlson

SE slope of Cerro Campana, *Lewis et al. 3110* (MO). Cerro Campana, *Luteyn 1060* (DUKE). Taboga Island, *Macbride 2771* (US). Cerro Campana, *Porter et al. 4319* (MO). El Espino de La Chorrera, *Rodriguez 34* (DUKE, PMA). Chivo-Chivo, *Solanilla 6* (MO, PMA). Taboga Island, *Standley 27904* (US). W slope of Cerro Campana, 2500 ft, *Tyson et al. 2381* (PMA). 9 km SE of El Valle de Antón, *Wilbur et al. 11165* (DUKE). Isla Taboga, 0–186 m, *Woodson et al. 1477* (MICH, MO). VERAGUAS: Santiago, 50 m, *Allen 1081* (MO, US). Ca. 5 mi NE of La Mesa, *Blum & Tyson 663* (MO). Carretera a San Francisco, *Cisneros 13* (MO, PMA). Santiago near San Francisco, *Dwyer 1240* (MO, US). N tip of Coiba Island, *Foster 1640* (DUKE). Between San Francisco and Santa Fé, *Stern et al. 1913* (US). Near Santiago, *Tyson 5175* (MO). Puerto Mutis, 12 mi S of Santiago, *Tyson 6021* (MO). PROVINCE UNKNOWN: *Duke 6191* (MO); *Weston 5709* (MO).

19. SCOPARIA

Scoparia L., Sp. Pl. 116. 1753. Gen. Pl., ed. 5. 52. 1754. TYPE: *S. dulcis* L.

Herbs or weak *shrubs*, much branched, glandular punctate, the branches slender, alternate. *Leaves* opposite, mostly small and narrow, apically dentate or entire, sometimes dissected, basally cuneate; petioles indistinct. *Inflorescence* 1–several flowered in the leaf axils, the pedicels filiform. *Flowers* small, the corolla white, blue or reddish, 4-lobed nearly to the base, 1 (posterior) lobe emarginate, glabrous outside, densely bearded inside with long hairs; stamens 4, alike, the filaments glabrous, inserted in the corolla tube, the anthers ovoid, versatile, exserted; ovary ellipsoidal or hemispheric, glabrous, the style glabrous, mostly short, the stigma punctiform, exserted. *Capsule* globose, dehiscing septicidally and loculicidally from the apex; seeds numerous, minute, reticulate.

Scoparia includes about 20 species, most of these in South America or Mexico. The species treated here is a pantropical weed. Some species are used for medicinal teas.

Literature:

Chodat, R. 1908. Étude critique des genres *Scoparia* L. et *Hasslerella* Chod. Bull. Herb. Boissier sér. 2, 8: 1–16; 85–89.

Fries, R. E. 1906. Systematische Übersicht der Gattung *Scoparia*. Ark. Bot. 6(9): 1–31, *tab.* 8.

———. 1908, 1909. Einige weitere Bermerkungen über die Gattung *Scoparia*. Bull. Herb. Boissier sér. 2, 8: 934–940.

1. **Scoparia dulcis** L., Sp. Pl. 116. 1753. TYPE: Jamaica, *Sloane*, not seen.—FIG. 18.

Perennial *herbs* or weak *shrubs* to 1.5 m tall, conspicuously glandular punctate (under a lens), the branches slender, angled by the concaulescent leaf bases, mostly glabrous, sometimes ciliate at the nodes. *Leaves* opposite, sometimes obovate, saliently dentate and to 4 cm long and 1.8 cm wide, mostly much narrower and smaller, the teeth often inconspicuous, apically obtuse, basally cuneate, sometimes with a distinct petiolar region, the midvein prominent with ca. 3 ascending lateral veins on each side, the venation often obscure above. *Inflorescence* of 1–several flowers from the leaf axils, often paired; pedicels

FIGURE 18. *Scoparia dulcis* L.—A. Habit (×3⅗).—B. Fruit (×3⅗). [After *White 116* (MO).]

filiform, mostly ca. 5 mm long. *Flowers* small, the calyx 4-parted nearly to the base, the lobes oblong, obtuse or rounded apically, mostly glabrous, sometimes ciliate, apically rounded, 3 nerved; corolla white, rotate, 4-lobed nearly to the base, the lobes 2½ mm long, only slightly exceeding the calyx, ovate, glabrous above but densely bearded with long white hairs in the lower ⅓ within; stamens 4, the filaments glabrous, slender, inserted on the corolla tube, 1 mm long; anthers yellow, 1 mm long, ellipsoidal, exserted; ovary ellipsoidal, the style 1.5 mm long, only slightly exceeding the anthers, the stigma punctiform, exserted. *Capsule* globose, 1.5–2.0 mm across, exceeding the calyx, 4-sulcate, yellowish brown, glabrous, dehiscing apically, sometimes beaked by remnants of the style; seeds numerous, ca. 0.5 mm long, somewhat prismatic, coarsely reticulate.

Scoparia dulcis is a widespread weed of tropical lowlands. The leaves are used for a tea, used in some countries as a beverage and in others as a medicinal. It is reputed to purify or cool stagnant water. "Sweet Broom," "Escobilla amarga," "Escoba amarga."

BOCAS DEL TORO: Almirante-Changuinola Canal, *Blum 1405* (MO). Without other locality, *Carleton 95, 149* (both US). Laguna de Chiriquí, *Hart 175* (US). Runway, Bocas del Toro, *Lazor et al. 2351* (MO, PMA). Changuinola to 5 mi S at junction of Río Terebé, 100–200 ft, *Lewis et al. 791* (DUKE, MO, PMA, US). Chiriquí Lagoon, *Wedel 1243, 1337* (both MO), *2830* (MO, US). CANAL ZONE: Pipeline Road near Gamboa, *Clewell & Tyson 3273* (PMA). Boyd-Roosevelt Highway near Babanita, *Croat 9274* (MO, SCZ). Lowland side of Ft. Kobbe, *Duke & Mussell 6589* (MO). Frijoles, *Ebinger 631* (MO). Chagres, *Fendler 5* (MO, US). Ancón Hill, *Greenman & Greenman 5123* (MO). Between Frijoles and Monte Lírio, 30 m, *Killip 12123* (US). Río Chagres bridge near Gamboa, *Lasseigne 4273* (MO). 2 mi N of Gatún Locks on road to Fort San Lorenzo, *Lazor & Blum 5421* (MO). Pipeline Road 16 mi N of Gamboa, *Lewis et al. 5444* (MO). Ancón, *Macbride & Featherstone 18* (US); *Piper 5537* (US). Gatuncillo, *Piper 5657* (US). Balboa, *Standley 25460* (US). Frijoles, *Standley 27637* (US). Río Pedro Miguel near East Paraiso, *Standley 30041* (US). Río Cocolí, Road K-9, *Stearn et al. 336* (MO). Near survival school, Curundu, *Tyson 1061* (PMA). Miraflores, *White 116* (MO). BARRO COLORADO ISLAND: *Croat 4160* (MO); *Ebinger 593* (MO); *Shattuck 49* (MO). CHIRIQUÍ: Llanos W of Gualaca, 500 ft, *Allen 5046* (MO). Quebrada Guanabanito 1 km W of dam at La Represa, Burica Peninsula, *Busey 485* (MO). Pozos de Salud, outskirts of Tolé Town, 330 m, *Correa 128* (DUKE, SCZ). La Repressa 2 mi SW of Puerto Armuelles, 0–200 m, *Croat 22064* (MO). David airport, 25 ft, *Lewis et al. 758* (MO). Quebrada Mellize 6 mi S of Puerto Armuelles, 0–150 m, *Liesner 420* (MO). Towards El Hato del Volcán ca. 8 km N of La Concepción, *Wilbur & Luteyn 19450* (DUKE). San Bartolomé, 0–50 m, *Woodson & Schery 926* (MO). COCLÉ: Natá, 50 m, *Allen 841* (MO, US). 12 mi NE of Penonomé, 1200 ft, *Lewis et al. 1526* (MO, US). Boca del Toabré at confluence of Río Coclé del Norte, *Lewis et al. 5492* (DS). 2 mi N of El Valle, 620–660 m, *McDaniel 8290* (DUKE). Mountains above El Valle, *Stimson 5021* (SCZ). 10 mi E of Natá at Río Grande, *Tyson 5302* (MO). El Valle on road to La Mesa, *Tyson 6920* (PMA). El Valle de Antón, *Wilbur et al. 11709* (DS, DUKE, MO). COLÓN: Road to Portobelo ¼ mi N of Maria Chiquita, *Croat 11358* (MO). Santa Rita Ridge, *Dwyer & Gentry 9356* (MO, PMA). Maria Chiquita E of Río Piedras toward Portobelo, *Dwyer & Kirkbride 7790* (MO). Under bridge crossing Chagres River 1 mi N of Colon-Panama line, *Lazor & Tyson 2960* (MO). Santa Rita Ridge 5.5–6 mi E of Transisthmian Highway, *Lewis et al. 5388* (DS, MO). Santa Rita Ridge road, *Mori & Kallunki 1822* (MO). 5–7 mi SW of Portobelo towards Maria Chiquita, *Wilbur & Weaver 11173* (DUKE). DARIÉN: Boca Quebrada Venado, Río Tuqueza, *Bristan 1100* (MO). Mannene, *Kirkbride & Bristan 1611* (MO). Town weed, Yaviza, *Lazor & Correa 3385* (PMA). Río Tuquesa at lower mining camp Charco Chiva, *Mori 6964* (MO). HERRERA: Roadside between El Potrero and Las Minas, *Croat 9656* (MO). Ocú, *Díaz 6A* (DUKE, MO, PMA). 1 mi N of Las Minas, *Wilbur et al. 12113* (DUKE). LOS SANTOS: Santa Ana, *Duke 12475* (MO). Río Tonosí, near Tonosí, *Lewis et al. 1572* (MO). Loma Prieta, Cerro Grande, 2400–2800 ft, *Lewis et al. 2239* (MO). Headwaters of Río Pedregal 25 mi SW of Tonosí, 2500–3000 ft, *Lewis et al. 2923* (DUKE, MO). Between Tonosí and Macaracas, *Oliver et al. 3563* (DUKE, MO). Monagre Beach 5 mi SE of

Chitré, *Tyson et al. 3043, 3049* (both MO). Pedasí, *Wilbur et al. 12035* (DUKE). PANAMÁ: Pedro Gonzales, Pearl Islands, *Allen* 2592 (MO). 7 mi N of Cerro Azul on road to Cerro Jefe, 2600 ft, *Blum 1804* (SCZ). Río Majé 4–5 mi above waterfall near Bayano Lake, *Croat 34686* (MO). 5–6 mi E of Chepo on Panamerican Highway, *Duke 4015* (MO). Savannas near Chepo, *Duke 6050* (DS, MO). Río Pacora just below Río Corso, *Duke 12017* (MO). Río Mar, *Dwyer 1802* (MO). Without other locality, *Grisebach 1857* (MO). Road to Cerro Azul, *Lazor* 5545 (SCZ). SW slope of Cerro Campana, *Lewis et al. 3135* (DUKE, MO). Chimán, *Lewis et al. 3305* (MO). Tributary of Río Chagres 5 mi SW of Cerro Brewster, 1000 ft, *Lewis et al. 3404* (DUKE, MO). Road to Cerro Campana 2–4 mi above Panamerican Highway, 800 m, *Luteyn 3999* (DUKE). Near Tapía River, Juan Díaz region, *Maxon & Harvey 6672, 6755* (both US). E of Bella Vista, *Maxon & Valentine* 6952 (US). Saboga Island, *Miller 1974* (MO, US). El Llano-Cartí Road, 916 km from Panamerican Highway, *Mori & Kallunki 1865* (MO). Sabanas, *Paul 43* (US). Chepo, *Pittier 4455* (US). Taboga Island, *Standley 27109* (US). Río Tapía, *Standley 28076* (US). Cerro Azul, 2000 ft, *Tyson 2100, 2126* (both MO). W slope of Cerro Campana, 2300 ft, *Tyson 4026* (MO). Chepo, *Tyson 6785* (MO, PMA). Carretera Cermeno a Monte Oscuro, *Varela 5* (MO). Veracruz, *Wendehake 12* (MO). Near Chepo, *Wilbur & Luteyn 11798* (DUKE). Cartí road ca. 5 km from Panamerican Highway, *Wilbur & Luteyn 19484* (DUKE); *Witherspoon & Witherspoon 8722* (MO). Isla Taboga, 0–186 m, *Woodson et al. 1431* (MO). SAN BLAS: E of Puerto Obaldía, *Croat 16937* (MO). Mulatuppa, Río Ibedi, *Duke 8506* (MO). Soskatupu, *Elias 1695* (MO). Caladonia Harbor, Mt. Vernon, *Elmore L14* (DS, US). Mainland opposite Achituppu, *Lewis et al. 107* (MO, US). Forests around Puerto Obaldía, 0–50 m, *Pittier 4365* (US). VERAGUAS: Stream feeding Laguna La Yeguada, 15 mi N of Calobre, 644 m, *Luteyn 1442* (DUKE, MO). Panamerican Highway ½ km W of turnoff to Ocú, *Nee 7999* (MO). 5 mi SE of Calobre, *Wilbur et al. 12126* (DUKE). Outskirts of Santiago, *Wilbur & Teeri 13009* (DUKE).

20. STEMODIA

Stemodia L., Syst. Nat., ed. 10: 1118, 1374. 1759. nomen cons. TYPE: *S. maritima* L.

Stemodiacra P. Browne, Civ. Nat. Hist. Jam. 261. 1756. nomen rejic. Based on *Scordium maritimum* Sloane (1707) = *Stemodia maritima* L.

Phaelypea P. Browne, Civ. Nat. Hist. Jam. 269. 1756. nomen rejic. prop. TYPE: *P. erecta; foliis sessilibus* . . . P. Browne = *Stemodia durantifolia* (L.) Sw.

?*Matourea* Aubl., Hist. Pl. Guiane 2: 641, 259, obs. p. 48. 1775. TYPE: *M. pratensis* Aubl. See Minod (1918: p. 202 in note).

?*Dickia* Scopoli, Intr. Hist. Nat. 199. 1777. Based on *Matourea* Aubl.

?*Angervillea* Necker, Elem. Bot. 1: 351. 1790. Based on *Matourea* Aubl.

Unanuea Ruiz & Pavón, Ic. Fl. Peru. ined. ex Benth. in DC., Prodr. 10: 380. 1846. in syn.

Unannea Steud., Nom. Bot. ed. 2. 2: 729. *Unanuea* Ruiz & Pavón, orth. but. TYPE: *U. febrifuga* Steud.

?*Chodatophyton*[12] Minod, Bull. Soc. Bot. Genève sér. 2. 10: 235. 1918. TYPE: *C. ericifolium* (Kuntze) Minod.

Lendneria[12] Minod, Bull. Soc. Bot. Genève sér. 2. 10: 240. 1918. TYPE: *L. humilis* (Solander) Minod = *Stemodia verticillata* (Mill.) Hassl.

?*Verena*[12] Minod, Bull. Soc. Bot. Genève sér. 2. 10: 250. 1918. TYPE: *V. hassleriana* (Chodat.) Minod.

?*Valeria*[12] Minod, Bull. Soc. Bot. Genève sér. 2. 10: 251. 1918. TYPE: *V. trifoliata* (Link) Minod.

Erect or sprawling *herbs*, the stems mostly pubescent, drying angled, branching freely. *Leaves* opposite or ternate, ovate or elliptical, mostly serrate, pubescent, often glandular punctate, petiolate, or subsessile. *Inflorescences* 1–3 flowers in the leaf axil, often geminate or ternate, the peduncles slender, ebracteate.

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[12] Minod based these genera on species formerly considered to belong to *Stemodia*. Only *Lendneria* was critically examined in this study, and it is properly considered a synonym of *Stemodia*. See discussion under *S. verticillata* below.

Flowers with the calyx 5-lobed to near the base, the lobes narrow, sometimes slightly unequal; corolla white, blue, or purplish, often drying dull orange, tubular to narrowly campanulate, 2-lipped, the upper lip entire, emarginate or 2-lobed, bearded in the throat, the lower lip 3-lobed, the tube often pubescent inside; stamens 4, the filaments mostly inserted in pairs at somewhat different levels, glabrous, 1 pair of anthers sometimes with thecae differing from the others, the thecae held apart by an enlarged globose or armlike connective, parallel or divaricate, sometimes pubescent, a staminode sometimes present; ovary smooth, conical, mostly compressed, the style terete, glabrous, the stigma ligulate, often with 2 minute but distinct lateral appendages; placentas drying to form a narrow peg which does not run to the top of the ovary, the septum, in the apical portion at least, remaining with the capsule walls, in the lower portion sometimes remaining with the placenta; dehiscing loculicidally and septicidally ½ way or all the way down; seeds small, numerous, oblong pyriform, often longitudinally 6–10 sulcate, the surface minutely rugose.

Stemodia includes about 35 species in the New World tropics. Several of these are of widespread distribution as ruderal or paludal weeds. The small pedicellate blue or white flowers, narrow corolla tube and deeply divided calyx are useful characters for recognition. The sulcate seeds are useful in recognizing at least two of the Panamanian species. The fact that the upper portion of the placental septum remains with the capsule walls and is not apparent after dehiscence separates it from *Lindernia* and some other genera.

Literature:

Minod, M. 1918. Contribution à l'étude du genre *Stemodia* et du groupe des Stémodiées en Amérique. Bull. Soc. Bot. Genève sér. 2. 10: 155–252.

a. Flowers subsessile, the pedicels less than 1 mm long; leaves not noticeably punctate.
  b. Leaves subsessile, basally auriculate and seeming to clasp the stem; stigmas recurved and flattened; plants often more than 15 cm tall; basal leaves mostly more than 10 mm long ---------- 1. S. *durantifolia*
  bb. Leaves conspicuously petiolate, basally cuneate; stigmas erect or slightly bent; plants mostly less than 15 cm tall; leaves mostly less than 10 mm long ---------- 5. S. *verticillata*

aa. Flowers long petiolate, the pedicels more than 5 mm long; leaves copiously glandular punctate beneath (under a lens).
  c. Stems soon glabrescent, leaves glabrous; flowers in open racemes; anthers pubescent ---------- 4. S. *reliquiarum*
  cc. Stems and leaves pubescent; flowers solitary or paired in the leaf axils; anthers glabrous.
    d. Corolla more than 9 mm long; leaves mostly more than 15 mm long ---------- 3. S. *peduncularis*
    dd. Corolla less than 9 mm long; leaves mostly less than 15 mm long ---------- 2. S. *jorullensis*

1. **Stemodia durantifolia** (L.) Swartz, Obs. Bot. 240. 1791. Based on *Capraria durantifolia* L.

Veronica caule hexandra . . . Sloane, Cat. Plant. Jamaic. 81. 1696; Voy. Isl. Madera . . . 196, *tab. 124, fig. 2.* 1707. TYPE: not seen.

Lysimachia coerulea galericulata . . . Sloane, Cat. Pl. Jamaic. 66. 1696; Voy. Isl. Madera . . . 174. 1707.

Phaelypea erecta; foliis sessilibus . . . P. Br., Civ. Nat. Hist. Jam. 269. 1756. Based on *Veronica caule hexandra* . . . Sloane. Cites also *Lysimachia coerulea galericulata* . . . Sloane.

Capraria durantifolia L., Syst. Nat. ed. 10: 1116. 1758 (May–June 1759). Based on *Lysimachia coerulea galericulata* . . . Sloane; *Capraria durantifolia* L., Pl. Jamaic. Pug. (Amoen. Acad. 97) 399. 28 Nov. 1759. Based on *Phaelypea erecta; foliis sessilibus* . . . P. Br.; *Capraria durantifolia* L., Syst. Veg. ed. Murray (ed. 13) 475. 1774; ed. Murray (ed. 14) 567. 1784.

C. oppositifolia L., Fl. Jamaic. (Amoen. Acad. 96) 380. 13 Dec. 1759. ?based on *Phaelypea erecta; foliis sessilibus* . . . P. Br.

Conobea verticillaris Spreng., Novi Prov. Hort. Acad. Hal. 13. 1818. TYPE: Cult. Berlin, from Brasil, not seen. fide Minod (1918).

Stemodia verticillaris (Spreng.) Link, Enum. Pl. Hort. Berol. 2: 144. 1822.

Conobea viscosa Schrank in Hornschuch, Syll. Pl. Nov. 2: 61. 1828. TYPE: not seen.

Stemodia chilensis Benth., Bot. Reg. 1470. 1831. TYPE: not seen.

Lobelia verticillata Kunze in Poepp., Coll. Pl. Chilenso Exsiccate ex Presl., Prodr. Mongr. Lobel. 52. 1836. nomen nudum. TYPE: Chile, *Poeppig 170* (MO). Not *Stemodia verticillata* (Mill.) Hassl.

?*Stemodia berteroana* Benth. in DC., Prodr. 10: 384. 1846. TYPE: Hispaniola, *Bertero* (?G, not seen; not G-DC.).

Stemodiacra durantifolia (L.) Morong, Pl. coll. Paraguay 183. 1880–1891, not seen, fide Minod (1918).

S. *chilensis* (Benth.) Kuntze, Rev. Gen. Pl. 2: 466. 1891.

?S. *berteroana* (Benth.) Kuntze, Rev. Gen. Pl. 2: 466. 1891.

S. *durantifolia* (Benth.) Kuntze, Rev. Gen. Pl. 2: 466. 1891.

Stemodia erecta (P. Br.) Minod, Bull. Soc. Bot. Genève sér. 2. 10: 212. 1918.

Erect, viscid-pubescent *herbs* to 1 m tall, branching freely, the stems compressed on emerging, somewhat woody below, slender above, drying angled, hispid with short, whitish, gland-tipped hairs. *Leaves* opposite, lanceolate, varying greatly in size on the same plant, the lower leaves often 4(–6) cm long, 10(–15) mm wide, the upper leaves mostly less than 2.5 cm long, 5 mm wide, apically acute, basally auriculate and clasping the stem, appearing perfoliate, serrate, the teeth sharply ascending, callose tipped, viscid with scattered erect, gland-tipped, slender hairs and sessile glands, the hairs somewhat longer beneath, the midvein prominent, the ca. 5 lateral pinnate veins on each side often obscure. *Inflorescence* solitary in the leaf axils, often geminate, sometimes aggregated to appear long spicate; pedicels short, to 0.5 mm long, drying angled, viscid pilose; 2 linear, opposed, pubescent, ca. 2 mm long bracts near the top of the pedicels. *Flowers* with the calyx 5-lobed nearly to the base, the lobes narrow, acute, costate, ca. 2 mm long, viscid pilose, somewhat accrescent in fruit; corolla blue or purplish, drying dark apically, 5–6 mm long, outside minutely puberulent and glandular upwards, 2-lipped, the upper lip ca. 2 mm long, truncate or slightly emarginate, bearded in the throat with sturdy clavate hairs, the lower lip 3-lobed, the lobes ca. 1.5 mm long, the stamens 4, the filaments glabrous, terete, inserted at about the same level just below the sinuses in the corolla tube, the lowermost pair somewhat longer, the anthers alike, the connective globose, separating the 2 parallel, basifixed, oblong thecae, the thecae ca. 0.6 mm long, broadly elliptical after dehiscence, light (?yellow) colored; ovary narrowly conical, septally sulcate, somewhat compressed, glabrous, eglandular, the style stout, terete, glabrous, the stigma compressed, fanlike, slightly downcurved, the stigmatic area terminal, linear. *Fruit* a conical or ovoid capsule ca. 3 mm long, at first dark (?purplish), ultimately stramineous, the placenta dark, narrowly compressed conical, 2–3 mm

long, loculicidally and septicidally dehiscent to the base; seeds ca. 0.3 mm long, ellipsoidal, blackish brown, tuberculate in lines.

This is the most widespread species in the genus, ranging from Arizona and California through the Antilles and Central America to Uruguay and Chile. In Panama it occurs as a ruderal or street weed in lowlands, especially in the Pacific drainage. It may be recognized by its auriculate-based, lanceolate leaves and clusters of small, subsessile flowers, thus somewhat resembling some species of *Hyptis*, e.g., *H. verticillata*.

CANAL ZONE: Near Boy Scout Camp, *Croat 12917* (MO). Mangrove swamp between Gatún and Fort Sherman, *Croat 15396* (MO). Curatella savanna W of Ft. Kobbe, *Duke & Mussell 6582* (MO). SE side of Madden Lake near the Puente Natural, *Nee & Hansen 14070* (MO). Between Miraflores and Pedro Miguel, 30–50 m, *Pittier 2504* (US). Balboa, *Standley 25618, 30903* (both US). Miraflores Lake, *White & White 197* (MO). Pipeline Road N of Gamboa, *Wilbur & Weaver 11223* (DUKE). COCLÉ: Between Porto Posada and Penonomé, *Williams 166* (NY, US). COLÓN: Mouth of Río Piedras, *Lewis et al. 3188* (MO). LOS SANTOS: Near Tonosí, *Duke 12492* (MO, OS). Río Tonosí near Tonosí, *Lewis et al. 1555* (MO, US). PANAMÁ: Without other locality, *Duchassaing* (P). By airstrip near beach in Panama City, *Duke 4005* (MO). Isla del Rey, *Duke 9572* (MO, OS). Between Río Pacora and Chepo, *Dwyer et al. 5116* (MO). Sabanas, *Heriberto 76* (US). Near Tapia River, Juan Díaz region, *Maxon & Harvey 6756* (US). La Jagua vicinity of Pacora River, 25–60 m, *McDaniel 10322* (MO). Sabanas N of Panama City, *Paul 581* (US). Sabana de Dormisolo near Chepo, 60–80 m, *Pittier 4665* (US). Agricultural Experiment Station at Matías Hernández, *Pittier 6880* (NY, US). Río Tapia, *Standley 28225* (US). Near Matías Hernández, *Standley 28898* (US). Between Las Sabanas and Matías Hernández, *Standley 31913* (US).

2. **Stemodia jorullensis** H.B.K., Nov. Gen. Sp. Pl. 2: 358. 1817. TYPE: Mexico, ?*Humboldt* (?P, not seen).

S. *xorullensis* Spreng., Syst. Veg. 2: 466. 1825. (1824) S. *jorullensis*, orth. mut.
S. *angulata* Oerst., Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 1853: 22. 1854. TYPE: Costa Rica, *Oersted* (?C, not seen).
S. *ageratifolia* Wright in Sauv., Fl. Cubana 99. 1873. TYPE: Cuba, *Wright 2993*, not seen.
Stemodiacra jorullensis (H.B.K.) Kuntze, Rev. Gen. Pl. 2: 466. 1891.
S. *angulata* (Oerst.) Kuntze, Rev. Gen. Pl. 2: 466. 1891.

Small annual *herbs*, erect, prostrate or ascending, to 30 cm tall, the stems slender, drying angled, sparingly pilose with weak, whitish hairs; roots short. *Leaves* opposite, broadly ovate, mostly 8–12 mm long, apically obtuse or rounded, basally truncate or cuneate, the margins serrate with ca. 8 blunt teeth on each side, some of the teeth double, venation pinnate with 4–5 veins on each side, above sparingly pilose with weak white hairs, beneath with a few similar hairs and punctate with sessile or plane glands; petiole narrow, broadening upwards, about ½ as long as the blade. *Inflorescences* 1–3 flowers in the leaf axils, the pedicels slender, pilose, much exceeding the leaves, ebracteate. *Flowers* with the calyx pilose, 5-lobed to near the base, 4 lobes alike and equal, narrowly acute, the fifth slightly longer, broader, apically differentiated; corolla white, perhaps with some pink, drying dull yellow or orange, 6–9 mm long, tubular, 2-lipped, glabrate outside, sometimes ciliate on the angles, the upper lip 2-lobed, the lobes broadly rotund, ca. 1.7 mm long, apically sinuate, bearded at the throat with stout, clavate hairs, the lower lip 3-lobed, the middle lobe obtuse, ultimately acute, the 2 lateral lobes rotund, the tube generally pilose within, sometimes with

a few scattered sessile glands; stamens 4, the anterior filaments basally geniculate, glabrous, inserted near the base of the tube, 5–6 mm free, the anthers alike or dissimilar, the thecae ca. 0.7 mm long, oblong, parallel, separated by the globose connective, the posterior filaments glabrous, ca. 1 mm free, inserted in the upper half of the corolla tube, the anthers similar to the anterior pair but slightly larger, a minute staminode inserted between the posterior filaments at the same level; ovary glabrous, smooth, eglandular, compressed, septally sulcate, the style straight, the stigma situated at the level of the lower (posterior) anthers, bent at an obtuse angle to the style, minutely appendaged on the sides. *Capsule* ovoid or ellipsoidal, about as long as the calyx, apically acute or obtuse, dehiscing septicidally and loculicidally from the apex, the valves apically recurving; placenta narrowly conical, dark, winged only at the base; seeds numerous, reddish brown, oblong, longitudinally ca. 6-sulcate, ca. 0.5 mm long.

This species grows in wet roadsides and marshes. It ranges from Mexico to northern South America, and it also occurs in the Greater Antilles. In most features it is similar to S. *peduncularis* but its stature, leaves, flowers and fruits are smaller. The glands on the leaf undersides are nearly plane whereas those of S. *peduncularis* are usually globular and distinctly raised from the leaf surface. The level of insertion of the stamens also differs markedly.

One collection examined, *Tyson & Smith 4145*, differs from the others in having narrowly elliptical leaves reaching ca. 1.2 cm in length. Details of the corolla and androecium do not differ from the other collections.

BOCAS DEL TORO: Chiriquí Lagoon, *Wedel 2576* (MO, US). CANAL ZONE: Chagres, *Fendler 215* (MO). Balboa, *Standley 29275* (US). CHIRIQUÍ: David, *Roy 2* (US). COCLÉ: Boca del Toabré at confluence with Río Coclé del Norte, *Lewis et al. 5554* (DS, MO). COLÓN: Portobelo, La Cruzio Trail, *Ebinger 102* (MO). Meadows around Portobelo, *Pittier 2442A* (US). DARIÉN: Boca de Cupe, 40 m, *Allen 899* (MO). Río Mortí ca. 6 mi upstream from Mortí Abajo, 100 m, *Duke 10160* (DUKE, MO, OS). Manene, *Kirkbride & Bristan 1569* (MO). Río Tuquesa at mining camp Charco Chiva, *Mori 6953* (MO). PANAMÁ: Cañita, *Tyson & Smith 4145* (MO).

3. **Stemodia peduncularis** Benth. in DC., Prodr. 10: 382. 1846. SYNTYPES: Mexico, *Linden 1098, Galeotti 1024* (both K, neither seen).—FIG. 19.

Stemodiacra peduncularis (Benth.) Kuntze, Rev. Gen. Pl. 2: 466. 1891.

Erect, sprawling or scrambling *herb* or *subshrub* to 1.5 m long, the stems slender, prominently angled, pubescent with weak short whitish hairs, the angles ciliate, ultimately stramineous near the base, spreading by stolons and sometimes rooting at the lower nodes. *Leaves* opposite, frequently with a short axillary shoot bearing 1–2 pairs of juvenile leaves to ½ as long as the expanded leaves, ovate, mostly 2–4 cm long, 1.5–2.5 cm wide, apically obtuse, basally truncate or cuneate, the margins conspicuously serrate with numerous blunt teeth, the venation pinnate with ca. 4 lateral veins on each side, these furcating near the margin and running into the teeth, the minor venation obscure above, drying reticulate beneath, pubescent above with numerous scattered short whitish weak, slightly appressed hairs, beneath with fewer but slightly longer hairs and numerous globular or depressed globular, amber, yellow or black glands; petioles slender

FIGURE 19. *Stemodia peduncularis* Benth. Habit (×⅗). [After *Davidson* 482 (MO).]

but slightly winged upwards, ¼–½ as long as the leaves, mostly copiously pubescent. *Inflorescences* 1–3 flowers fasciculate in the leaf axils, sometimes geminate, the peduncle slender, puberulent to tomentose, becoming glandular upwards, ebracteate, the pedicels to 20 mm long, ½ to as long as the subtending leaf. *Flowers* with the calyx 5-lobed to near the base, the lobes narrowly deltoid to subulate, subequal, ca. 5 mm long, pubescent and glandular dorsally, basally cucullate, the tips slightly differentiated; corolla 12–18 mm long, tubular, white, sometimes pinkish in part, red veined, drying dull orange, conspicuously nervate, 2-lipped, the upper lip 2-lobed, the lobes rotund, densely bearded just above the throat with stout hairs, and sometimes with a few glands outside, the lower lip 3-lobed, the lobes ca. 2 mm long, narrowly obtuse, the middle lobe narrower, the tube pilose outside especially near the top, the inside bearded on the upper side about ½ way up the tube and long pilose at the base; stamens 4 in 2 pairs, the anterior pair alike, the filaments inserted about ⅓ way up the tube, glabrous, ca. 2 mm free, the anther thecae oblong, ca. 0.7 mm long parallel, separated by the enlarged, discoid connective, the posterior pair of filaments subequal, inserted ca. 2 mm from the bottom of the tube, glabrous, 5–6 mm free, the anthers situated at the throat, the thecae unlike, unequal, smaller than those of the anterior pair, separated by a smaller enlarged connective; ovary smooth, glabrous, eglandular, narrowly conical, compressed, septally sulcate, the style straight, smooth, glabrous, the stigma obtuse, compressed, flanked by 2 small lateral projections, the stigmatic area terminal. *Fruit* ovoid, ca. 7 mm long, dehiscent septicidally and loculicidally part way down, at first dark ?purple, ultimately stramineous; seeds not seen.

Stemodia peduncularis ranges from Panama to Mexico (Vera Cruz). It is distinguished by its long pedicellate flowers, ovate leaves, and relatively long flowers. In Panama it occurs at middle and upper elevations in the Chiriqui Mountains.

CHIRIQUÍ: NE side of Cerro Pando, 7.8 air km NW of El Hato del Volcán, *Cochrane et al. 6308* (MO). E side of Cerro Pando, 6000 ft, *D'Arcy & D'Arcy 6648* (MO). Bajo Mono, Boquete District, 4500 ft, *Davidson 482* (MO, US). Slopes NE of Cerro Pando NW of Nueva California, 1500 m, *Wilbur et al. 11017* (MO).

4. **Stemodia reliquiarum** D'Arcy.[13] TYPE: Panama, *D'Arcy 10893* (MO, holotype; isotypes G, PMA).—FIG. 20.

Sparingly branched, sprawling *herbs*, the stems weak, drying dark brown, sulcate, angled below, sparingly pilose with weak, erect, 5-celled hairs, soon glabrescent; roots slender, weak, drying sulcate or compressed. *Leaves* opposite, ovate, mostly 3–5 cm long, 15–25 mm wide, apically acute or obtuse, basally obtuse or truncate, serrate with 10–15 teeth on each side, some of the teeth often double or irregular, the main venation 3–5 digitate, plane or prominulous above, elevated beneath, the central vein with 3–5 arcuate lateral veins, the venation

[13] *Stemodia reliquiarum* D'Arcy, spec. nov. *Herba* pusilla inconspicua; foliis ovatis, serratis, venis 3–5-digitatis; *inflorescentibus* terminalibus racemosis; floribus minutis, calycis 5-partitis, pilosis, corollis coeruleis salverformibus, staminibus binatim, pari supra fertili, antheris barbatis, infra rudimentali; seminibus stemodiis alis similibus.

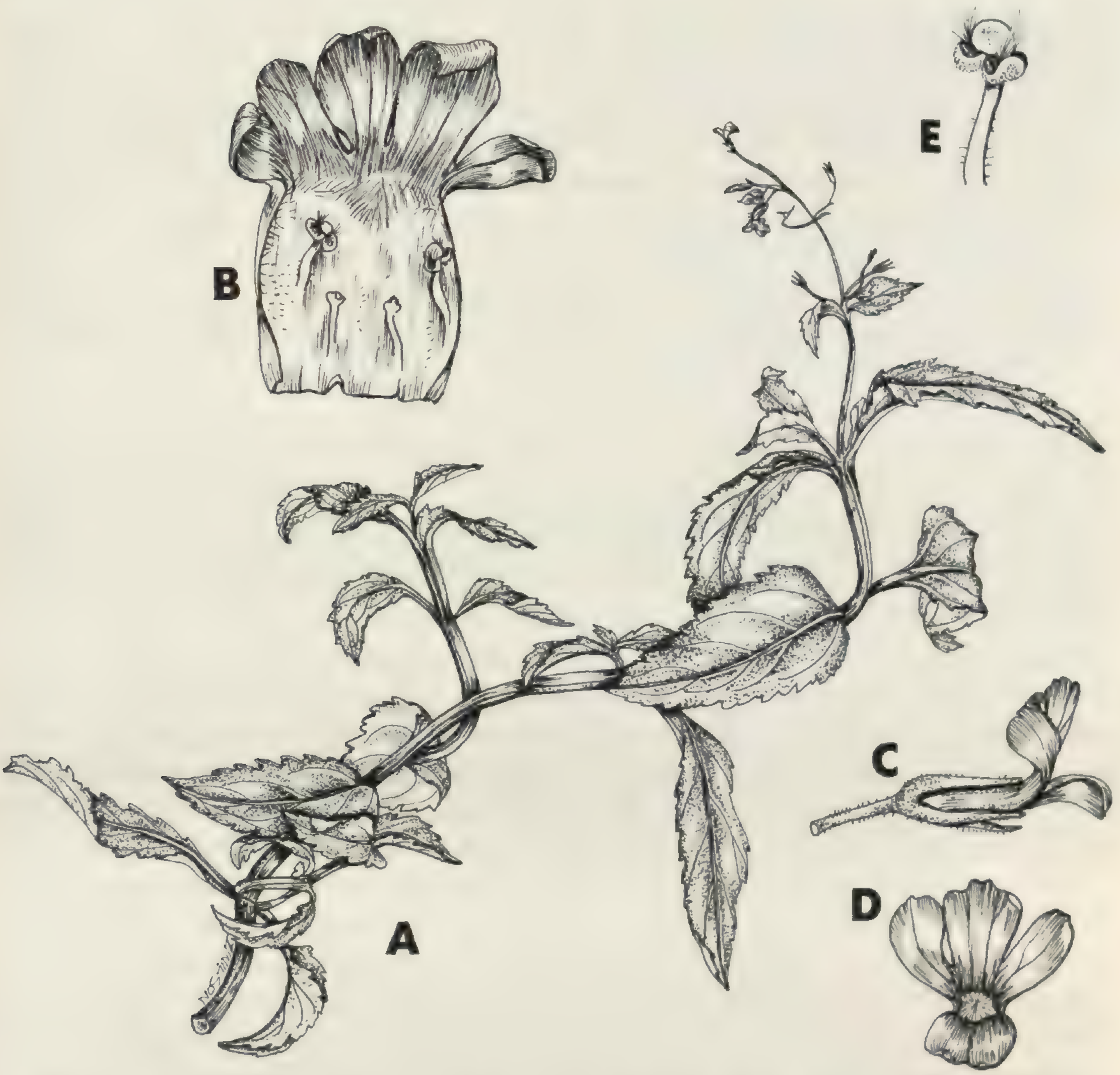

FIGURE 20. *Stemodia reliquiarum* D'Arcy.—A. Habit (×3⅗).—B. Corolla opened showing stamens (×8⅖).—C–D. Flower showing lateral and frontal views (×5⅖).—E. Stamen showing pubescent anther (×15). [After *D'Arcy 10893* (MO).]

anastomosing near the margin to form a continuous but sinuous submarginal vein, minor venation reticulate, prominulous on both sides but often obscure, glabrous, both sides punctate with minute pustules (?glands); petiole slender, narrowly margined, mostly 5–8 mm long, the bases forming decurrent angles on the stem just below the nodes; stipules wanting. *Inflorescence* a terminal, open raceme; pedicels slender, sparingly pilose, ca. 5 mm long, becoming 10–15 mm long in fruit, broadening slightly in the upper ½; bracts 2, basal, minutely foliaceous to scalelike, narrow, ciliate. *Flowers* small, the calyx 5-parted to the base, the segments narrow, 2–3 mm long, becoming 4 mm long in fruit, drying dark brown, sparingly pilose dorsally or ciliate, glabrous ventrally except at the very base, minutely callose apically, the 3 longitudinal veins evident ventrally; corolla blue, salverform, the tube 3–4 mm long, slightly exceeding the calyx, nervate, outside glabrous or with a few small hairs at the top, within apically densely tufted with

large hairs, pubescent below along 1 side with smaller hairs, the lobes porrect, slightly oblique, subequal, oblong, apically sinuate, 2–3 cm long, enervate, minutely pulverulent near the base ventrally; stamens 4, the lower pair of filaments ca. 0.5 mm long, inserted equally ca. 1 mm from the corolla base, the anthers much reduced, the thecae unequal, separated by the subcapitate connective but not by arms, opening laterally longitudinally by a large porelike slit, perhaps sometimes sparingly polleniferous, the upper pair of filaments 0.7–1.0 mm long, drying slightly compressed, inserted 1.0–1.2 mm from the corolla base, apically sharply down curved and expanded into an armlike connective, 1 anther theca sessile on the connective, and the other terminal on the stipelike connective arm, both thecae pulverulent outside, conspicuously tufted along the apical edge of the insertion on the connective, opening longitudinally into portlike slits; ovary conical, sulcate, the style short, stout, 0.5 mm long, the stigma clublike, perhaps down curved, about twice as wide as the style. *Fruit* a conical-obtuse capsule slightly exceeding the calyx, dehiscing apically into 4 valves, the placenta broad, unwinged; seeds numerous, prismatic, dark brown, longitudinally reticulate with narrow walls, ca. 0.6 mm long.

This species is diagnostically distinct from other members of *Stemodia* by its pubescent anthers. It is also amply distinct in superficial appearance; the ovate leaves, sprawling habit, terminal, open racemes and digitately nerved leaves are all good distinguishing features, and might warrant recognition at the generic level. *Stemodia reliquiarum* does not conform to any of the genera or infrageneric groups recognized by Minod in his study of the *Stemodia* alliance.

Although herbarium specimens reveal plants several decimeters long, in the field plants appear much smaller, as only the minute flowers of the open inflorescence are evident amongst the mass of other greenery which obscures the full size of this plant. Known only from grazed pastures in forest remnants on the Chiriqui mountains at about 2,000 m elevation, this species may be expected in other parts of Central America and perhaps northern South America.

CHIRIQUÍ: Disturbed cloud forest at Monte Rey above Boquete, *Croat & Porter 15678* (MO). Weedy pasture at Monte Rey, above Boquete, 1500–2500 m, *D'Arcy & D'Arcy 6391* (MO); *D'Arcy 10893* (MO). Wet soil on edge of forest, foot of Sierra del Boquete, 1200 m, *Maurice 702* (MO). COSTA RICA: CARTAGO: Tapanti Hydroelectric Reserve Trail along Río Dos Amigos, 1600–1700 m, *Croat 36214* (MO).

5. **Stemodia verticillata** (Miller) Hassl., Contr. Fl. Chaco (Trab. Mus. Farmac. Fac. Ciencias Méd. Buenos Aires 21): 110. 1909.

Erinus verticillatus Miller, Gard. Dict. ed. 8. 1768. TYPE: America, *Houston*, not seen.
Stemodia parviflora Aiton W. T., Hortus Kew. ed. 2. 4: 52. 1812. Based on *Erinus verticillatus* Mill.
Lindernia verticillata Britton in Britton & Wilson, Bot. Porto Rico 6: 184. 1925.
Lendneria humilis (Solander) Minod, Bull. Soc. Bot. Genève sér. 2. 10: 241. 1918.
Capraria humilis Solander, in Aiton W. T., Hortus Kew. ed. 1. 2: 354. 1789. TYPE: not seen. fide Sprague, Kew Bull. 1921: 211. 1921.
Stemodia humilis (Solander) Dawson, Revista Mus. La. Plata, Secc. Bot. 8: 14. 1956. not *S. humilis* Minod (1918).
Stemodiacra verticillata (Miller) Kuntze, Rev. Gen. Pl. 2: 466. 1891.
Stemodia arenaria H.B.K., Nov. Gen. Pl. 2: 357, *tab. 175*. 1817. TYPE: Colombia, *Bonpland* (?P, not seen).

?*Conobea pumila* Spreng., Novi Prov. Hort. Acad. Hal. 13. 1819. TYPE: Cult. Berlin, from Brasil, not seen. fide Minod (1918); Sprague 1921: 211. 1921.
Stemodia verticillata (Miller) Sprague, Kew Bull. 1921: 211. 1921. redundant combination.
?*Poarium veronicoides* Desv. ex Hamilton, Prodr. Pl. Ind. Occ. 46. 1825. TYPE: Hispaniola, Desvaux, not seen.
Herpestis diffusa Willd. ex Cham. & Schlecht., Linnaea 3: 6. 1828. TYPE: herb. Willd. 11444 (B, not seen; microfiche MO), in syn.
Stemodia pauciflora Rusby, Mem. Torrey Bot. Club 6: 93. 1896. *S. parviflora* Ait., orth. mut.

Erect or sprawling diminutive *herbs* to 15 cm tall, the stems slender, freely branching, drying angled, pilose with weak translucent hairs. *Leaves* opposite or ternate, broadly ovate, mostly 10–15 mm long, 8–12 mm wide, apically rounded or obtuse, basally cuneate to truncate, the margins conspicuously serrate with 7–9 teeth on each side, the teeth often double, the venation pinnate with ca. 4 lateral veins on each side, sparingly pilose on both sides, soon glabrescent above, not noticeably punctate or glandular; petioles about ½ as long as the leaves, slender but broadening upwards, pilose above, pubescent beneath. *Inflorescences* solitary in the leaf axils, often geminate or ternate, the pedicels short, ca. 1 mm long, drying angled, ebracteate. *Flowers* with the calyx 5-lobed to near the base, the lobes alike, linear, separate, costate, hyaline margined, 3 mm long, glandular pilose, corolla blue or purplish with a white eye, tubular, 5 mm long, 2-lipped, the upper lip truncate, apically sinuate or emarginate, saccate, puberulent outside, the inside bearded at the throat with stout, whitish clavate, unicellular hairs, the lower lip 3-lobed, the lobes truncate, glabrate, the tube white with dark lines, ciliate on the angles, slightly curved, otherwise glabrate outside, the inside generally pubescent on the dorsal side and near the bottom with long slender unicellular hairs; stamens 4 in 2 pairs, the ventral pair inserted ca. 1 mm above the bottom of the corolla tube, free ca. 2 mm, glabrous, the thecae reduced, ca. 0.15 mm long, parallel, separated by the somewhat enlarged connective, the dorsal pair inserted slightly unequally slightly above the ventral pair, 1 mm free, the thecae strongly divaricate, separated by the enlarged connective, 0.3 mm long, a short staminode inserted at the base of the tube between the 2 dorsal anthers; ovary glabrous, smooth, narrowly ovoid conical, compressed, the style stout, short, 1.0–1.5 mm long, basally expanded, the stigma compressed obtuse with conspicuous lateral appendages, ultimately recurving. *Fruit* a globose capsule ca. 1.25 mm across, dehiscing loculicidally and septicidally as far down as the septum (ca. ½ way down), the style persistent on 1 valve, the placenta ellipsoidal, ca. 1 mm long, extending little more than ½ the length of the capsule, punctate, the septum thickening, indurate below, the lower ½ persistent with the placenta and the lower ½ of the capsule, above narrow, and not persisting after dehiscence; seeds oblong to pyriform, 0.5 mm long, brownish yellow, longitudinally ca. 8 sulcate, the surface minutely rugose.

Minod (1918) segregated this species from *Stemodia* as the monotypic genus *Lendneria*, calling attention to a slightly different corolla shape, and a capsule dehiscent only ½ way down. These differences appear to be elaborations of trends evident in other species of *Stemodia* and do not suggest a differentiation of generic magnitude. The general configuration of the style, structure and insertion of the androecium, and longitudinal furrowing and minutely textured

surface of the seeds are all consistent with the variability of taxons recognized within *Stemodia*.

This species ranges from Mexico to Argentina, and it is present in the Antilles. It occurs as a weed of cultivation and other disturbance. It is reputed to have medicinal uses. "Hierba santa" (Costa Rica); "Corrimiento" (Salvador).

BOCAS DEL TORO: Nievecita, *Woodson et al. 1858* (MO, NY). CANAL ZONE: Pipeline Road to 18 km N of Gamboa, *D'Arcy 10636A* (MO). Chagres, *Fendler 216* (MO). SE side of Madden Lake near Puente Natural, *Nee & Hansen 14077* (MO). Cerro Gordo near Culebra, *Standley 26037* (US). Sosa Hill, Balboa, *Standley 26490* (US). Río Paraíso above East Paraíso, *Standley 29886* (US). Summit, *Standley 30137* (US). Fort Sherman, *Standley 30945* (US). Barro Colorado Island, *Standley 41004* (US). DARIÉN: Boca de Cupe, 40 m, *Allen 897* (MO, US). LOS SANTOS: Río Tonosí near Tonosí, *Lewis et al. 1580* (MO). PANAMÁ: Sabanas N of Panama City, *Paul 588* (US). Isla Taboga, *Woodson et al. 1468* (MO, NY). SAN BLAS: Between Cangandí and Mandinga, *Duke 14755* (MO, OS).

21. TETRANEMA

Tetranema Benth. ex Lindl., Bot. Reg. 29: *tab.* 52. 1843. nomen cons. (contra quid?). TYPE: *T. mexicana* Benth. ex Lindl. = *T. roseum* (Mart. & Gal.) L. Wms. non *Tetranema* Sweet, Hort. Brit., ed. 2. 149. 1830 (Leguminosae) nomen nudum, nec. *Tetranema* J. Areschoug, Nova Acta Regiae Soc. Sci. Upsal. ser. 2. 14: 418. 1850 (Algae).

Allophyton Brandegee, T. S., Univ. Calif. Publ. Bot. 6: 62. 1914. TYPE: *A. megaphyllum* Brandeg. = *Tetranema megaphyllum* (Brandegee, T. S.) L. O. Williams.

Suffruticose *herbs*, erect or sprawling, the stems stout, sometimes woody, puberulent or glabrous. *Leaves* opposite, subentire to dentate, the major veins pinnate, the minor venation sometimes conspicuously reticulate; petiole basally clasping, sometimes obsolete. *Inflorescence* axillary, scapose or racemose cymose, the flowers crowded, the pedicels short in flower, sometimes elongating in fruit, subtended by narrow bracts. *Flowers* with the calyx 5-lobed part way down, the lobes narrow, the limb campanulate, angled; corolla campanulate, purplish, the upper lip sinuate or retuse margined, the lower lip 3-lobed, the lobes all spreading; stamens 3–4, didynamous, the anthers 2-celled, the staminodes sometimes present; style slender or thick, the stigma capitate or rotate. *Capsule* ovoid, or globose, glabrous, loculicidal; seeds numerous, angled.

Tetranema includes five species of moist forests of Central America. All species are rare and few collections have been made. Only the species treated here is known to occur south of Guatemala.

Literature:

Pennell, F. W. 1925. The genus *Allophyton* of southern Mexico and Guatemala. Proc. Acad. Nat. Sci. Philadelphia 72: 269–272.

Williams, L. O. 1972. Tropical American Plants XII (*Tetranema* pp. 127–132). Fieldiana, Bot. 34: 101–132.

Tetranema bicolor L. O. Williams, Fieldiana, Bot. 34: 127. 1972. TYPE: Nicaragua, *Bunting & Licht 748* (F, not seen).—FIG. 21.

FIGURE 21. *Tetranema bicolor* L. O. Williams. Habit (×½). [After *Dressler 5039* (MO).]

Perennial *herbs*, the stems sprawling or erect, stout and somewhat woody, at first strongly compressed, soon terete, drying dark brown, pulverulent, the nodes conspicuous. *Leaves* opposite, sometimes unequal, elliptical or obovate, to 19 cm long, 8 cm wide, apically short acuminate, basally acuminate, the margins subentire with faint suggestions of unevenly spaced teeth, the costa and lateral veins drying conspicuous beneath, ca. 8 on each side, at first straight and ascend-

ing, arcuate in the marginal area, anastomosing to form a loop-connected submarginal vein which gives rise to short continuations to the margin, membranous, dark green and glabrous above, light green with arachnoid pubescence beneath, sparse on the lamina but copious and appressed on the veins, the petiole slender, to 3 cm long, narrowly winged upwards merging into the lamina, slightly expanded and clasping basally, dark brown, pulverulent. *Inflorescences* axillary, contracted few-flowered racemes appearing umbellate or capitate, the peduncle slender, 6–60 mm long, green, slender, compressed and sulcate, minutely pulverulent puberulent, decorticate and stramineous in age, the pedicels subtended by unequal pairs of narrowly deltoid or lanceolate bracts, 12–18 mm long; pedicels short, obscured by the bracts, to 10 mm long in fruit. *Flowers* with the calyx narrow, 14–18 mm long, 5-lobed about ⅓ of the way down, the lobes narrow, acute, the tube campanulate, strongly angled, obscurely puberulent on the angles, slightly narrowed upwards, not accrescent; corolla campanulate with the posterior (upper) lip oblong, obtuse and retuse, ca. 4 mm long, the lower lip 3-lobate, the lobes oblong ovate, obtuse; stamens didynamous, the anthers 2-celled, the staminode ?absent; style slightly thickened, the stigma entire, rotate. Mature *capsule* unknown.

This species is known only by the type collection and those cited below. No corollas were seen and the fruit is unknown. Details of the corolla, androecium and gynoecium were taken from Williams' original description. *Tetranema bicolor* is easily mistaken for a member of the Gesneriaceae; the repent habit, membranous, discolorous leaves and stout stems are unlike other members of the Panamanian Scrophulariaceae. However, the crowded calyces, which somewhat resemble depauperate bladders of *Physalis*, are a good character for determination.

The plant figured by Williams has leaves in unequal pairs with narrowed winged bases which clasp the stem, while in the Panamanian plants seen, the leaf bases are so narrowly winged as to appear petiolate and the leaves are about equal. The position and length of the peduncle is variable within the Panamanian material.

COCLÉ: 7 km N of El Copé, 700–850 m, *Folsom et al. 7085* (MO, PMA). La Mesa, 2 km W of Cerro Pilon, 860 m, *Sullivan* 523 (MO). VERAGUAS: 15–20 km NW of Santa Fe between Escuela Agrícola Alto Piedra and continental divide, 650–800 m, *Dressler 4731* (MO). Lower slopes of Cerro Tute, Escuela Agrícola Alto Piedra 7–8 km NE of Santa Fe, 750–850 m, *Dressler 5039* (MO).

22. TORENIA

Torenia L., Sp. Pl. 619. 1753; Gen. Pl., ed. 5: 270. 1754. TYPE: *T. asiatica* L.

Nortenia Thouars, Gen. Nov. Madag. 9. 1808. LECTOTYPE: *N. thouarsii* Cham. & Schlecht. = *Torenia thouarsii* (Cham. & Schlecht.) Kuntze.

Erect or decumbent *herbs*, freely branching, the stems angled and sulcate, sometimes pubescent. *Leaves* opposite, serrate or crenate, petiolate, pinnately veined. *Inflorescences* 1–3 flowers in a leaf axil, sometimes geminate or ternate, the pedicel angled, subtended by a basal, linear bract. *Flowers* with the calyx united to near the top, wing angled, sometimes conspicuously so, somewhat

accrescent in fruit, enclosing the capsule, the corolla campanulate to tubular salverform, the upper lip erect, the lower (closed) lip with 3 rotund lobes, bearded in the throat, stamens 4 in 2 pairs, the filaments inserted near the top of the tube, the dorsal pair arching upwards and holding the anthers above the stigma and the ventral pair, the anthers alike or the dorsal pair reduced, the connectives coherent in pairs, the thecae oblong to linear, divaricate, held apart by the connectives, a staminode present; ovary smooth, the style straight, the stigmas flattened together. *Capsule* dehiscing septicidally to the base, the placenta linear, conspicuously winged by the stramineous septum; seeds globose, yellow, tuberculate.

Torenia is an Old World genus of perhaps 50 species. The species treated here are introduced. Several species other than *T. fournieri* are cultivated for ornament and may appear from time to time in Panamanian gardens.

Torenia is closely allied to *Lindernia* and *Stemodia*, but has been kept separate by Old World workers, e.g., Philcox (1968). It differs from *Stemodia* in its calyx shape and its placental septum, and from *Lindernia* in a number of small details. Although the seeds are pitted or tuberculate in *Torenia* and some species of *Lindernia* and *Stemodia*, the pitting does not appear to be of the same kind.

a. Calyx becoming more than 5 mm wide (including wings); corolla showy, the limb more than 8 mm across, the tube conspicuously exserted from the calyx ---------- 1. *T. fournieri*

aa. Calyx less than 5 mm wide; corolla small, the limb less than 6 mm across; the tube scarcely exserted from the calyx ---------- 2. *T. thouarsii*

1. **Torenia fournieri** Linden in Fourn., Illustr. Hortic. 23: 129, *tab.* 249. 1876. TYPE: Cochin China, not seen.—FIG. 22.

Decumbent or erect *herb*, to 30 cm tall or 60 cm long, freely branching; stem 4-angled and sulcate, often reddish, sparingly ascending pilose with white hairs. *Leaves* opposite, ovate, to 5 cm long, apically acute, basally obtuse or short cuneate, the margins serrate to crenulate, the venation pinnate with 5–6 arcuate veins on each side, sparingly pubescent on each side; petioles slender, 8–15 mm long. *Inflorescences* solitary flowers in the leaf axils, sometimes geminate, the pedicels sulcate, glabrate, sometimes broadening upwards, 10–20 mm long, each with a basal bract, sometimes linear, 1–2 mm long, sometimes foliose. *Flowers* showy, the lower lip 3-lobed, the lateral lobes deep purple, the middle lobe lighter colored with a large yellow eye, rotund, ca. 10 mm wide, sinuate or subentire, the upper (ventral) lip pale, often bluish, 1-lobed, somewhat larger than the lower lip, minutely puberulent outside, bearded in the throat; dorsal filaments arching above the style and ventral anthers, the anthers with the thecae oblong cuneate, ca. 1 mm long, strongly divaricate, subtended by the cuneate connective, the connectives coherent in pairs; style straight, the stigmas discoid ovate to deltoid, flattened together, ciliate and dorsally ascending pubescent near the margin, situated slightly above the ventral anthers.

Torenia fournieri is native to Southeast Asia and is occasionally cultivated for ornament. The flowers are showy and resemble pansies, trinitarias (*Viola*,

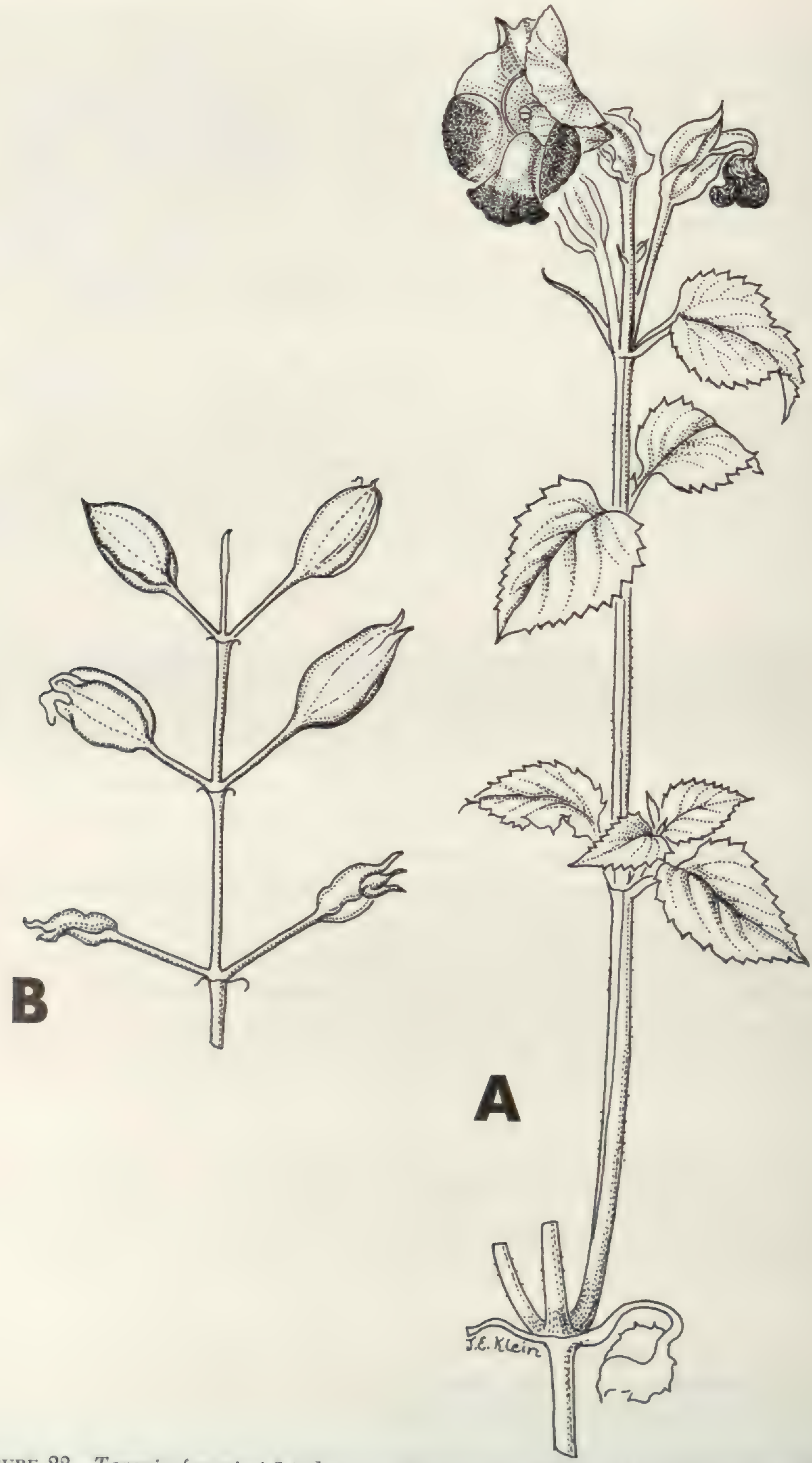

FIGURE 22. *Torenia fournieri* Linden.—A. Habit in flower (×1).—B. Fruiting inflorescence (×1). [After *Standley* 28846 (US).]

sp.). The common name, Wishbone Flower, stems from the configuration of the stamens just outside the corolla throat.

Standley (1928) reported this species as naturalized in Panama. As only one collection is known from the country, it may not have persisted. However, it may be expected in gardens from time to time, grown from imported seed. Several horticultural forms are known, including several dwarf forms and one with white flowers.

CANAL ZONE: Mount Hope Cemetery, *Standley 28846* (US).

2. **Torenia thouarsii** (Cham. & Schlecht.) Kuntze, Rev. Gen. Pl. 2: 468. 1891.

Nortenia thouarsii Cham. & Schlecht., Linnaea 3: 18. 1928. Based on *Torenia pedunculata* Willd., ined. LECTOTYPE: Madagascar, *Du Petit-Thouars* (B-Willd. 11547, not seen, microfiche MO).

Torenia parviflora Hamilt. in Wall. Cat. no. 3958 ex Benth., Scroph. Ind. 39. 1835, nomen illegit., notes *Nortenia thouarsii* Cham. & Schlecht., as syn.

T. nortenia Steud., Nom. Bot. ed. 2. 2: 692. 1841. Based on *Nortenia thouarsii* Cham. & Schlecht.

Lindernia thouarsii (Cham. & Schlecht.) Edwin, Phytologia 19: 361. 1970.

Ascending *herb* to 20 cm tall, the stems branching freely, slender, drying sulcate, sparingly glandular on emerging, soon glabrescent; roots short and fibrous. *Leaves* opposite, lanceolate to ovate, apically obtuse or acute, basally obtuse, rounded or truncate, the margins crenate serrate with ca. 6 teeth on each side, mostly 1.5–2.5 cm long, 8–12 mm wide, the venation pinnate with ca. 3 pairs of strongly ascending arcuate veins on each side, glabrate but ciliolate with short, white trichomes at the margins and on the main veins beneath, obscurely glandular punctate beneath; petiole 2–7 mm long, the margins ciliate, especially at the base. *Inflorescence* 1–3 flowers in the leaf axil, sometimes geminate or ternate; peduncles glabrate, sulcate, exceeding the petioles, 5–15 mm long, the bracts basal, linear, 1–2 mm long, ciliate. *Flowers* with the calyx tubular, narrowly ovoid or pyriform, with narrow, ciliolate wing angles, with 5 short lobes, somewhat accrescent in fruit; corolla slightly exserted from the calyx, bluish, purplish or whitish, tubular, ca. 10 mm long, 5-lobed, the lobes rotund, erose crenulate, ca. 2 mm across, bearded in the throat with stout whitish clavate hairs; stamens 4, the ventral pair inserted near the corolla mouth, the filaments geniculate, with a sterile, linear extension from the point of insertion, ca. 1.5 mm free, the anthers somewhat reduced, the thecae separated by the connective, rotund, the dorsal pair inserted ca. 1 mm below the ventral pair, the filaments arching above the style and not geniculate, anthers 0.8 mm free, the thecae separated, divaricate, ca. 1.7 mm long, the connectives somewhat glandular, coherent holding the 2 anthers together; staminode inserted between and slightly above the filaments bearing a small globose antheroid; ovary narrowly conical, smooth, glabrous, the style straight, terete, the stigmas discoid, erose, flattened together, ca. 0.7 mm long. *Capsule* narrowly ovoid conical, scarcely exserted from the calyx, dehiscing septicidally to the base.

Torenia thouarsii is native to the Indian Ocean area but is naturalized in the New World tropics, occurring in Trinidad and from Peru to Costa Rica and the

lower Oronoco in Venezuela. The elongate, tubular calyx and linear placenta are good recognition characters.

BOCAS DEL TORO: Island potrero, Changuinola Valley, *Dunlap* 342 (PH, US).

23. VERONICA

Veronica L., Sp. Pl. 9. 1753. TYPE: *V. officinalis* L.

Annual or perennial *herbs*, often prostrate or ascending; stems terete or angled, often branching at the base. *Leaves* opposite, at least below, mostly pubescent with simple, multicellular hairs or glandular hairs; petioles distinct or not. *Inflorescences* either in alternate-bracted elongate racemes or solitary flowers in the axils of terminal unmodified leaves. *Flowers* mostly small, the calyx divided nearly to the base, the 4(5) lobes mostly narrow, entire, often exceeding the flowers; corolla rotate or campanulate, blue or white, rarely yellow, somewhat lobed; stamens 2, the anthers exserted; style straight, the stigma capitate. *Capsule* flattened perpendicular to the septum, the carpels discoid or lenticular, marginally connate, loculicidal or sometimes septicidal; seeds numerous, variously ornamented.

Veronica is a genus of over 200 species mainly of temperate parts of the Old World, but a few species are native to the Americas. They are frequently encountered in temperate regions as weeds of fields, streets or roadsides. The species in Panama are distinguishable from one another by many conspicuous characters but elsewhere species are sometimes difficult to separate.

a. Pedicels longer than the flowers, fruits or leaves; all leaves and bracts opposite; corolla more than 3 mm across; leaves with substantial petioles ..... 3. *V. polita*
aa. Pedicels shorter than the flowers, fruits or leaves; only lower leaves opposite; upper bracts alternate; corolla less than 3 mm across; leaves subsessile.
  b. Capsule ciliate; flowers blue; calyx pubescent, the hairs eglandular; style more than 0.5 mm long ..... 1. *V. arvensis*
  bb. Capsule glabrous or with a few gland-tipped hairs; flowers white; bracts glabrous or with gland-tipped hairs; style less than 0.5 mm long ..... 2. *V. peregrina*

1. **Veronica arvensis** L., Sp. Pl. 13. 1753. TYPE: Herb. Linn. (LINN 26.57 or 26.58, neither seen, microfiche MO).

Ascending annual *herbs*, usually branching at the base; stems pubescent in lines with weak, whitish hairs; roots fibrous, to 25 cm long. *Leaves* opposite, obovate, apically obtuse or rounded, toothed, basally cuneate, to 1.5 cm long, pubescent on both sides with weak, multicellular hairs, petiole 0.5–1.0 mm long, flattened. *Inflorescences* long leafy appearing racemes; pedicels 0.5–1.0 mm long; bracts oblong or lanceolate, ca. 4 mm long, costate, entire or basally dentate, pubescent. *Flowers* small, the calyx divided nearly to the base, the lobes oblanceolate, entire, costate, pubescent, exceeding the corolla, ca. 4 mm long, slightly accrescent in fruit; corolla campanulate, blue with a minute white eye, ca. 2 mm long, the stamens 2, the style straight, ca. 0.6 mm long, glabrous, stigma minute, capitate. *Capsule* margins ciliate, otherwise glabrous, stramineous, the valves ultimately wide spreading; seeds reddish brown, ca. 1 mm long, ellipsoidal.

Veronica arvensis grows in pastures and lawns, often prostrate in part but usually with some parts ascending, the ascending portions often consisting only of "leafy" racemes. The blue flowers are minute but evident. The species is of Old World origin but is naturalized throughout most of the Americas. In Panama it has been found only in upland Chiriqui.

CHIRIQUÍ: Between Cerro Punta and Guadalupe, 1980 m, *Wilbur et al. 13046* (DUKE, MO). Town of Cerro Punta, *Wilbur et al. 15338* (DUKE).

2. **Veronica peregrina** L., Sp. Pl. 14. 1753. TYPE: Herb. Linn. (LINN 26.58 or 26.57, not seen, microfiche MO).

Erect or ascending annual *herbs*, the stems branching, glabrous or pubescent, sometimes glandular; roots fibrous. *Leaves* opposite, ovate, elliptical, oblong or lanceolate, often very variable in size and shape on the same plant, entire, costate, the strongly ascending lateral venation mostly obscure, glabrous to short pilose. *Inflorescences* long terminal leafy appearing racemes, the pedicels ca. 1 mm long, the bracts ovate or oblong, to 10 mm long, entire, much exceeding the flowers. *Flowers* with the calyx divided nearly to the base, the lobes entire, much exceeding the flowers, ovate or oblong, costate, glabrous or basally puberulent with short glandular hairs; corolla white, campanulate, stamens 2, the style short, less than 0.25 mm long, the stigma capitate. *Capsule* glabrous, stramineous, 2–3 mm long.

Veronica peregrina is native to the Americas but is naturalized in most parts of the Old World as well. In Panama it has been collected only in upland Chiriqui. Glabrous plants are sometimes designated as var. *peregrina*, while plants with copious glandular pubescence are referred to as var. *xalapensis* (H.B.K.) Pennell. Pennell (1935) stated that the two varieties intergrade over wide areas. The Panamanian collection are glabrate.

CHIRIQUÍ: Garden weed, Cerro Punta, *Godfrey 67328* (MO). Bambito, 5600 ft, *Tyson 7185* (PMA). Valley of upper Río Chiriquí Viejo, *White 328* (MO, PH). Between Cerro Punta and Guadelupe, 1980 m, *Wilbur et al. 13052* (DUKE). La Garita, ca. 3 km WNW of Cerro Punta, 2000 m, *Wilbur et al. 15272* (DUKE).

3. **Veronica polita** Fries, Novit. Fl. Suec. 1. 1819. TYPE: Sweden, *Fries* (?UPS, not seen).—FIG. 23.

Prostrate or occasionally ascending annual *herbs*, branching at the base, rooting at the lower nodes, the stems drying angled, sparingly pilose. *Leaves* opposite, broadly ovate or elliptical, apically obtuse, basally truncate, conspicuously dentate in the upper ⅔, mostly 10–18 mm long, the veins ca. 5, subdigitate, strongly ascending; petiole to 8 mm long, about ½ as long as the leaves. *Inflorescences* solitary flowers in leaf axils near the branch apices; pedicels slender, exceeding the leaves, pilose; bracts not differentiated. *Flowers* with the calyx divided to the base, the lobes oblong to lanceolate, pubescent, ca. 4 mm long; corolla rotate campanulate, blue with a conspicuous white eye and lines to the center; stamens 2, the filaments stiff, the anthers bluish, the style stiff, the stigma punctiform. *Capsule* evenly pubescent overall, the carpels plump, ca. 3 mm long.

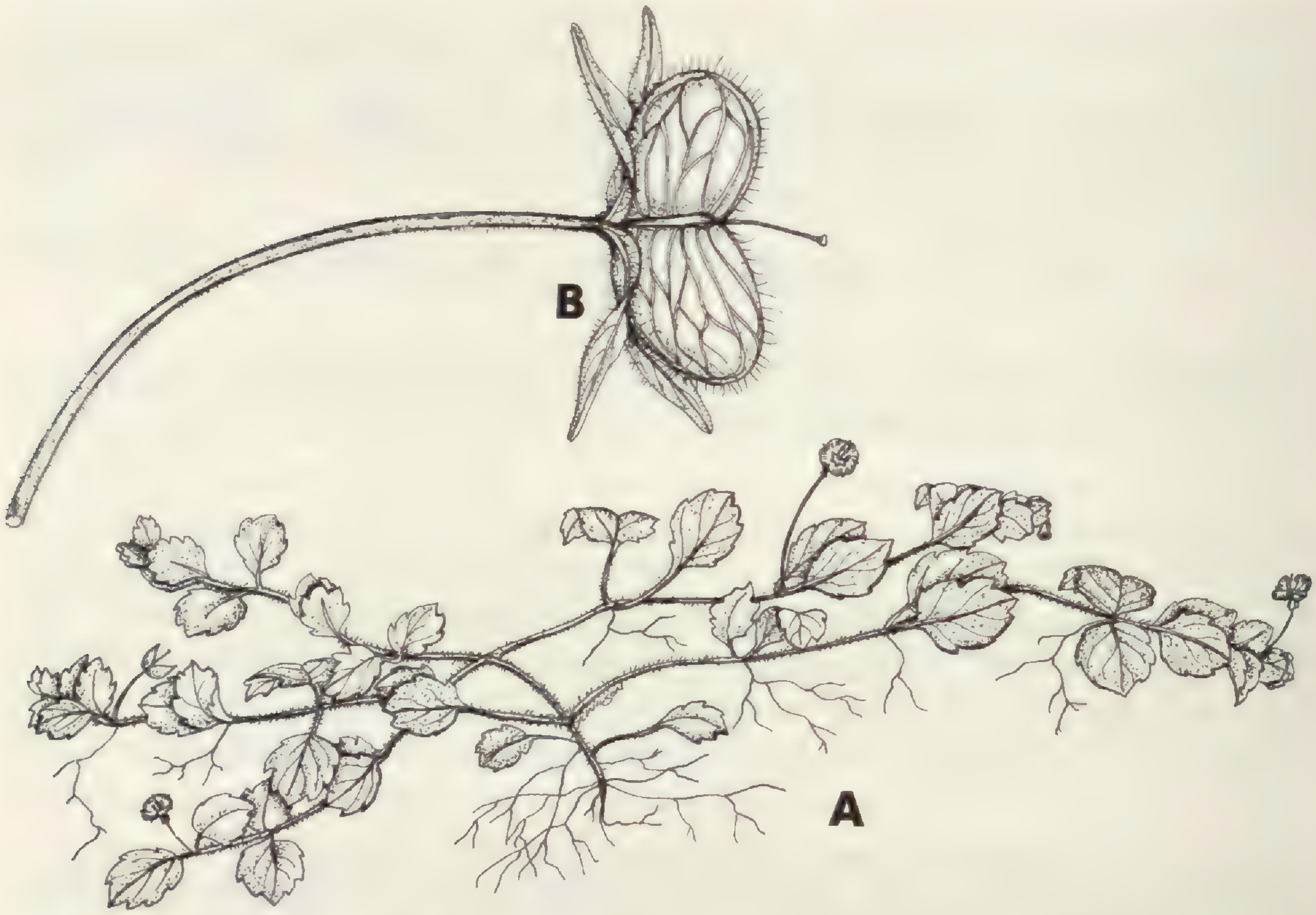

Figure 23. *Veronica polita* Fries.—A. Habit (×½).—B. Capsule (×4). [After *Tyson 7122* (PMA).]

Veronica polita is native to Europe and the mediterranean region but is now widely naturalized in the New World. It occurs in cultivated fields and lawns. In Panama it is known only from upland Chiriqui.

CHIRIQUÍ: Cerro Punta, 6000 ft, *Tyson 7122* (PMA).

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THE BOTANY AND NATURAL HISTORY OF PANAMA

A symposium to signal completion of the Flora of Panama will be held in Panama 1–4 April 1980. Sessions will include the physical setting, archaeology, vegetation, flora, fauna and demography of Panama and nearby countries as well as other natural history related topics. Conservation of endangered landscapes will be a theme. Both invited and contributed papers will be given, and either Spanish or English may be used. Limited funds may be available to assist costs of attending this meeting. The symposium is sponsored jointly by the Missouri Botanical Garden, the University of Panama, and the Smithsonian Tropical Research Institute.

Contact: Prof. Mireya D. Correa A.
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ANNALS
OF THE
MISSOURI BOTANICAL GARDEN

VOLUME 66 1979 NUMBER 3

BIOGEOGRAPHY OF THE BEES[1, 2]

CHARLES D. MICHENER[3]

ABSTRACT

Bees are most abundant and diverse in certain warm temperate, xeric regions of the world, especially the Mediterranean basin, the Californian region, and coniguous desertic areas. Other warm temperate xeric areas, like central Chile or the western part of southern Africa, have less rich faunas. Arid tropical regions, as well as tropical savannas, have poor bee faunas. For example, the southern margin of the Sahara and northern Australia are not rich in bees, in spite of the nearness of the former to the Mediterranean basin with past nondesert connections to the Mediterranean and the contiguity of the latter with the large warm temperate Australian faunal area. Equatorial savannas like those of east Africa are rather poor in bees.

Warm temperate, mesic areas, such as those of eastern North America, Europe, or the southern Brazilian to Argentina region of South America, also have rich faunas, although less so than do the Mediterranean basin and southwestern United States. Perhaps because of its small area, the climatically equivalent region in South Africa (largely in Natal) has a fauna that is best described as depauperate tropical, with certain temperate elements, but without great richness.

The moist tropics vary considerably in abundance and diversity of bees. In the Americas, they are almost or quite as rich as are the warm temperate mesic areas, but in Africa the fauna is far poorer, although richer than that of the Oriental region. There is a single Paleotropical bee fauna, richest in Africa and progessively smaller as one goes eastward across southern Asia to New Guinea, the Solomon Islands, and northeastern Australia. The poverty of the Oriental faunal region is shown by the number of genera and subgenera—89 compared to 175 in sub-Saharan Africa and 315 in the Neotropics (including temperate areas).

Thus unlike many groups which abound in the tropics, bees attain their greatest abundance in warm temperate areas. It is especially in such areas, principally xeric ones, that certain presumably archaic groups of bees have survived, and it is likely that various groups originated in such areas.

---

[1] Contribution number 1665 from the Department of Entomology, University of Kansas, Lawrence, Kansas 66045, U.S.A.

[2] I am indebted to Dr. Peter H. Raven, Director of the Missouri Botanical Garden, for the stimulus that led me to prepare this paper, a summary of which was presented at the Annual Systematics Symposium held at the Missouri Botanical Garden on October 15, 1977. Dr. Raven also contributed many useful suggestions for improvement of the manuscript. I also appreciate the comments and criticisms on the manuscript generously given by George W. Byers, E. Gorton Linsley, David W. Roubik, and Jerome G. Rozen, Jr., and the editorial attention and careful typing of Mrs. Joetta Weaver.

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The poor tropical African fauna as compared to the tropical American fauna may be due to the greater effects of past aridity in Africa (tropical savannas are poor bee habitats), and also to the inavailability of good faunas in nearby warm temperate areas. Southern Africa provides a much smaller source than the temperate South American area. The savanna (now desert) barrier isolating tropical Africa from the Mediterranean coast is much more developed than the xeric barrier isolating tropical America from temperate North America.

There is no close relationship between the number of species of bees in an area and the number of species of angiosperms. Thus the tropics with extremely rich floras have only moderate bee faunas. On a more local level, the same is true. For example, there is no extremely rich bee-faunal counterpart to the Cape flora of South Africa. On the other hand, floras and bee faunas are not independent of one another.

The percentage of oligolectic bees appears to vary with the number of species in flight at a given time. It is thus highest in the arid, warm temperate areas where climatic conditions lead to simultaneous flowering of many kinds of plants, hence simultaneous activity of many kinds of bees. Under such circumstances oligolecty should decrease competitive interactions among the bees; it should also increase pollinator effectiveness for the plants.

Specialist (oligolectic) bees must often be limited in distribution by the ranges of the plants from which they feed. However, plants are ordinarily not limited in distribution by the ranges of their oligolectic pollinators, for even obligate outcrossing plants apparently usually are adequately pollinated by generalist pollinators. Indeed some oligolectic bees have little or no significance as pollinators and are in effect parasites or predators on pollen.

Bees arose from sphecoid wasps after the appearance of probably beetle-pollinated primitive angiosperms. The place of origin is unknown but might have been the arid interior of west Gondwanaland (Africa, South America), an idea in accordance with the current abundance of bees in dry areas and the southern distribution of primitive groups of bees. The small bee faunas and lack of endemic archaic types on New Zealand and New Caledonia may indicate that there were no bees when this area separated from Gondwanaland before the middle of the upper Cretaceous. Distributions of archaic types in temperate parts of southern continents indicate an origin early enough for bees to have dispersed on the fragments of Gondwanaland, although narrow intercontinental seas may well have existed before such bee groups arose. The earliest fossil bees are Eocene, by which time there were already highly specialized long-tongued families. A moderate amount of time before the Eocene must have been necessary for the probably rapid initial radiation of the bees.

Bee faunas of oceanic islands indicate that minute bees are sometimes carried by winds for long distances, and that bees of all sizes that nest in wood or dead stems are also relatively likely to make major dispersal steps across water. Moderate sized and large ground nesting bees are less likely to jump major barriers, yet related species of such bees are found in New Zealand and Australia, indicating relatively recent dispersal across the water. In general, however, bees are rather sedentary and do not readily cross major barriers. Nonetheless many genera dispersed between North and South America before continental connections were established, no doubt inhabiting islands that existed between these continents during most of the Tertiary. The present Antillean fauna gives an idea of the groups of bees capable of such island-hopping. At least two large groups, the Nomadinae and the Exomalopsini-Ancylini, show evidence of an origin in South America and Tertiary spread probably via islands to North America, and thence to Eurasia.

Some major groups of bees (e.g., Colletidae, Fideliidae, Exomalopsini, Nomadini) appear from their distributions to have had their origins or at least major early evolutionary radiation in southern continents. Others (e.g., Andreninae, Dufoureinae, probably Halictini) are equally attached to the Laurasian continents.

Most bee taxa have distributions which they could have attained with continents in their present positions, i.e., if they exist on more than one continent, they are on connected or nearby continents. This suggests that their dispersal has been relatively recent. Some taxa, however, show notable disjunctions, suggesting antiquity.

Some of the patterns of disjunction are as follows:

a. African-Oriental. Usually rather closely related tropical forms, probably isolated largely because of aridity of rather recent origin in southern Saudi Arabia, Iran, Pakistan, and northwestern India.

b. Western hemisphere amphitropical. Various taxa occur in temperate South America and also in North America, usually in the Sonoran and Chihuahuan regions, but not in the intervening tropics. Arid epochs combined with long distance dispersal must have been responsible

for such distributional patterns. There is some evidence that the north-to-south dispersal of amphitropical taxa was older than the south-to-north dispersal.

c. Asian-Australian. Few taxa, closely related in the two continents, suggest relatively recent dispersal; this route was opened by the approach of the continents and the appearance of intervening islands in the Miocene.

d. Xeric areas of North America, Central Asia, and South Africa (the *Hesperapis* group).

e. Largely xeric areas of Australia and North America, a few species in Central America and Colombia (*Hackeriapis-Chelostomoides*).

f. Pantropical in various combinations. The Meliponinae (several taxa) are the only pantropical bees (except for taxa that occur also in temperate areas). They have little ability to disperse across water gaps and since a modern genus occurred in the Eocene, the subfamily probably acquired its present distribution at least partly through the break-up of Gondwanaland. Some modern genera and subgenera must have existed in the uppermost Cretaceous.

g. Austral. The primitive family Colletidae is enormously better developed in temperate Australia than elsewhere. The tribe Paracolletini occurs not only in Australia but also in South Africa and temperate South America. The primitive family of long-tongued bees, Fideliidae, is limited to arid parts of southern Africa and Chile. These disjunctions may date to the end of the Cretaceous when water gaps among the southern continents were narrow, although cool temperate forms might have passed on land between South America and Ausralia via Antarctica as late as the end of the Eocene.

The time may seem premature for a paper on distributional history of bees in the sense that studies now under way on the cladistic relationships among bees will probably add to what can be said. In another sense, however, it is well to summarize our biogeographical knowledge of the group now, for biogeography is more than distributional history. Relations to climate and food resources (flowers), areas of abundance and diversity, means of dispersal, and the like are all related to biogeography and can be examined with or in part without detailed cladistic knowledge. Such information should be viewed with the cladistic findings, as they become known.

This paper consists of an examination of the distributions of major groups of bees (Hymenoptera, Apoidea), together with speculations as to the historical and ecological explanations of such distributions. Emphasis is placed on disjunct distributions, since they often shed special light on the historical factors involved.

Except for the section on relative abundance, for which numbers of species are used, the method is to examine the bees at the levels of genus and subgenus, usually without differentiating the two. (Thus if in a region there are three genera, one of them divided into four subgenera, I report six genera and subgenera for that area.) This procedure is used because different specialists, working with different groups and in different areas, have divided the bees differently; the groups regarded by some as subgenera are called genera by others. This problem does not disappear if one considers genera and subgenera as constituting a single classificatory level, but it is reduced. I have further reduced it by recognizing or not recognizing some groupings on the basis of personal knowledge and unpublished information. For the numbers of species reported in Table 1, I have sometimes made similar adjustments when synonymy or new species reported after a faunal study would considerably influence the figure given, or when it seems likely that subspecies will prove to be of specific status. The references in Table 1 are usually to the principal faunal studies; supplements except when very important are commonly not cited in order to avoid excessive expansion of the bibliography, but for Europe, the main area where supplements are a problem, most

are cited by Stoeckhert (1933). For areas where little revisional work has been done, I have sometimes used the number of species in a faunal list without adding any of the subsequently described species, thinking that synonymy will ultimately more or less balance the number of new species. Thus for Australia, while numerous new species of minute bees have been described since the major list of names was published in 1965, much synonymy remains to be recognized and published. Although the actual numerical data (numbers of genera and subgenera or of species) are somewhat shaky, relative numbers, whenever compared, have been evaluated and are believed to be good indices of the diversity at the genus-subgenus level in the areas or taxa being compared. The same applies to numbers of species, except that the unevaluated factor of intensity of collecting is even more important in this case.

The area of origin or of major radiation of a group cannot necessarily be recognized by its present area of greatest diversity or abundance. Nonetheless, in the materials below, I have frequently suggested that a taxon originated in or radiated in a certain continent or faunal area. Such speculation can be justified only when supported by other data, such as absence of the group in surrounding areas, and is always tentative, i.e., a hypothesis to be supported or rejected by other data.

Areas of Diversity and Abundance

For many groups of organisms, the tropics are the areas of maximum numbers of genera and species and of maximum morphological diversity. For this reason many groups are said to have originated in the equatorial regions, although the current restriction of tropical climates to those regions has not characterized climates through the evolutionary history of most major groups of organisms. Bees, however, appear to attain their greatest abundance, greatest numbers of species, and probably greatest numbers of genera and subgenera, not in the tropics, but in various warm temperate, xeric regions of the world (Michener, 1941, 1954; Linsley, 1958).

It is easy to make statements such as the above but to provide suitable documentation for them is difficult. The taxonomic literature is a poor guide because of our different levels of knowledge of different areas. In many parts of the world unnamed species are abundant. In some regions, like Africa, there are prodigious numbers of synonyms, mostly not yet recognized as such. One can better compare numbers of species taken in limited areas where bee specialists have worked for many years, because most of the species will be recognized, even if not properly identified, in such a study. A problem is that such areas differ in size and local vegetational, edaphic, and topographic diversity, and the bee specialists differ in the vigor with which they have sought to survey their local faunas. Thus differences in the faunas as published may result in part from factors other than genuine faunal differences. Similar problems exist if one compares faunal lists for larger areas—states, countries, etc. The data given below, however, give some idea of the number of species in certain regions. The greatest problem is scarcity of data outside of the Palearctic and Nearctic regions, so that claims of relatively poor tropical faunas are not abundantly substantiated. In my own experience collecting bees in tropical areas, however, I have been impressed

by the relative scarcity of bees (individuals and species) compared to their abundance in xeric, warm temperate regions. (The richest tropical areas are those of the Americas, and are a possible exception to this statement in terms of numbers of species.)

Table 1 lists some of the faunal studies that have been made, arranged by biogeographical areas. More or less continent-wide lists or catalogues have not been included (except for Australia), since they cover areas of such size and climatic diversity that they contribute nothing to the recognition of centers of abundance and faunal diversity.

The bee fauna is particularly rich in the Mediterranean basin and thence eastward to central Asia, and in the Madrean region of North America (=Californian and the desertic regions of the southwestern United States and northern Mexico). This richness is only indicated vaguely for the Palearctic region in Table 1, for there are no adequate studies of local faunas in the areas concerned. The large fauna of Spain (1,043 species recorded by Cebellos, 1956, without very detailed collecting or intensive studies) suggests such richness, but Spain includes diverse areas, high montane habitats to Mediterranean macchia, so that some Spanish species are boreal or mid-European rather than Mediterranean. The large fauna of southwestern France (491 species recorded by Pérez, 1890) is also indicative of the rich Mediterranean bee fauna. Local faunas in the Mediterranean area may contain over 300 species, and with careful collecting the number might in some places exceed 400 (see Graeffe, 1902, for the Trieste area).

For the equivalent Nearctic region, the Madrean, the enormous bee fauna of California is impressive, but California includes even more climatic zones than Spain. Part of the large size of the Californian fauna is due to the large area, north-south extent, and altitudinal and precipitational range found within the state. In the chaparral or macchia region, i.e., the area having a Mediterranean climate, however, the fauna is large, as shown by 439 species from the vicinity (within 16.6 km = 10 miles) of Riverside. Palm Springs, on the interface between such an area and the Sonoran desert, has an even larger bee fauna (probably about 500 species) thanks in part to local topographic and vegetational diversity.

Eastward through desert and arid steppe, from the Mediterranean Basin to central Asia, and from the Californian region to Texas, faunas are also rich. There are few faunal reports in these areas, but data do exist for some outlying regions. Northern and more humid prairie and steppe regions like North Dakota have only moderate-sized bee faunas. Popov's (1967a) report of 305 species from central Asia is probably rather incomplete; Pesenko's (1971–1975) 347 species from the Lower Don is probably more complete. The large lists of species from New Mexico and Wyoming (both assembled without detailed collecting, although that from Wyoming includes species from neighboring states) indicate rich bee faunas.

Moldenke (1976a, 1976b) has compared the bee faunas of various vegetational areas in California and the Pacific northwest. He finds the chaparral or macchia areas and the sparse forests of the southern mountains, i.e., the Californian areas of Mediterranean climate, richest in bee species, the Californian deserts (north-

TABLE 1. Some faunal studies of bees, indicating the number of species reported for various areas.

A. *Palearctic Region*	
Spain (Cebellos, 1956)	1,043
France (Gaulle, 1908)	769
Britain (Saunders, 1896; Richards, 1937)	240
Holland (Benno, 1969)	328
Switzerland (Frey-Gessner, 1899–1912)	458
Denmark (Jørgensen, 1921)	217
Germany (Stoeckhert, 1954)	566
Hungary (Friese, 1893a)	505
European USSR (Osychnyuk et al., 1978)	950
Finland (Elving, 1968)	230
Ireland (Stelfox, 1927)	80
Iceland (Petersen, 1956)	1
Regional and Local Lists	
Arctic Norway (Sparre-Schneider, 1909)	26
Bedfordshire, England (Chambers, 1949)	159
Devon, England (Perkins, in Stelfox, 1927)	181
Southwestern France (Pérez, 1890)	491
Nord & neighboring regions, France (Cavro, 1950)	327
Saone-et-Loire, France (Marchal, 1893)	141
Haute-Marne, France (Frionnet, 1905)	155
Suisse Romande (Beaumont, 1960)	114
Parc National Suisse (Beaumont, 1958)	201
Neuchâtel, Switzerland (Beaumont, 1955)	261
Northwest Germany (Stoeckhert, 1933)	263
Köln (= Cologne) (Aerts, 1949)	266
Mangfall region (Brassler, 1959)	366
Franken (Stoeckhert, 1933, 1954)	443
Amrum Island (Haeseler, 1976)	64
Bremen (Alfken, 1939)	288
Baden (Strohm, 1924; Stoeckhert, 1933)	399
Nassau (Buddeberg, 1895; Wolf, 1955)	348
Sachsen (Krieger, 1894; Stoeckhert, 1933)	340
Mecklenburg (Friese, 1893b; Tiede, 1917)	238
Brandenburg (Schirmer, 1911; Stoeckhert, 1933)	329
Thüringen (Rapp, 1945)	390
N. W. Thüringen (Blüthgen, 1916)	219
Pommern (Blüthgen, 1919, 1942)	273
Ostpreussen (= East Prussia) (Alfken, 1912a)	240
Westpreussen (= West Prussia) (Alfken, 1912b)	294
Schlesien (Ducke, 1898, 1900; Stoeckhert, 1933)	347
Prov. Poznan (= Posen) (Torka, 1913; Stoeckhert, 1933)	276
Poznan (Banaszak, 1973)	132
Puniny Natl. Park, Poland (Dylewska, 1962; Dylewska & Noskiewicz, 1963)	173
Tirol, Austria (Schletterer, 1887)	372
Dept. Zemplén, Hungary (Chyzer, 1886)	253
Trieste coastal region (Graeffe, 1902)	366
Trieste, Italy (Graeffe, 1890, 1895)	269
Southwest provinces of Finland (Valkeila, 1962)	195
Ukrainian Carpathians (Osychnyuk, 1967)	172
Bashkirskaja ASSR (Nikiforuk, 1957)	331
Steppes of Lower Don, USSR (Pesenko, 1971–1975)	347
Central Asia (Popov, 1967a)	305
Obihiro, Hokkaido, Japan (Usui et al., 1976)	82
Minami, Gifu Prefecture, Japan (Yamauchi et al., 1974)	57
Bonin Islands (Yasumatsu, 1955)	8

TABLE 1. Continued.

B. *Nearctic Region*	
California (Moldenke & Neff, 1974)	1,985[a]
New Mexico (Cockerell, 1906)	551
Wyoming (Lavigne & Tepedino, 1976)	663
Eastern USA (Mitchell, 1960, 1962)	859
North Dakota (Stevens, 1949–1952)	244
Michigan (Mitchell, 1960, 1962)	403
North Carolina (Mitchell, 1960, 1962)	521
Regional and Local Lists	
Northern Ellesmere Island (Richards, 1973)	2
Riverside, Calif. (P. H. Timberlake, in litt., 1950; Linsley, 1958)	439
Palm Springs, Calif. (P. H. Timberlake, in litt., 1950)	±500
Boulder County, Colo. (Cockerell, 1907)	186
Western Wisconsin (Graenicher, 1935)	184
Eastern Wisconsin (Graenicher, 1935)	217
Chicago region (Pearson, 1933)	169
Carlinville, Illinois (Robertson, 1929a)	297
Hattiesburg, Miss. (Michener, 1947)	103
Miami, Florida (Graenicher, 1930)	64
C. *Oriental Region*	
Java (Friese, 1914; M. A. Lieftinck, in litt.)	193
Philippines (Baltazar, 1966)	233
Micronesia (Krombein, 1950)	26
Solomon Islands (Krombein, 1951)	24
Fiji (Fullaway, 1957)	8
Samoa (Perkins & Cheesman, 1928)	13
Hawaiian Islands (Perkins & Forel, 1899)	54
Local List	
Barrackpore, Bengal (Rothney, 1903)	73
D. *Australian Region*	
Australia (Michener, 1965a)	1,618
E. *Neotropical Region*	
Costa Rica (Friese, 1916, 1921, 1925)	230
Panama (Michener, 1954)	353
Cuba (Alayo Dolmau, 1973)	107
Surinam (F. N. Dingemans-Bakels, in litt.)	293
Regional and Local Lists	
Barro Colorado Island, Panama Canal Zone (Schwarz, 1934a, 1934b)	76
St. Vincent & Grenada (Ashmead, 1900)	36
Belém, Brazil (Ducke, 1906)	251
Paraná, Brazil (3 localities) (Laroca, 1974)	255
Mendoza, Argentina (Jörgensen, 1912)	230
Desertic parts of Chile (Moldenke, 1976b)	176
Mediterranean climatic areas of Chile (Moldenke, 1976b)	183

[a] Moldenke & Neff (1974) actually list 2,042 species and subspecies. I have omitted a few extralimital ones and some subspecies that are unlikely to be recognized later as species. However, Moldenke (1976a) on different pages gives the number of species of bees in California as "1,000+" and as 1,200, without explaining the major difference from the earlier work in which the species were listed by name. In another paper (1976b) he gives the total number of bee species in the Pacific slope from Baja California to southern Alaska as 1,974.

western part of the Sonoran region) nearly as rich, and the boreal forests, grasslands, and the coastal zone progressively poorer. The actual numbers of species vary greatly according to how he divides the area, but representative numbers are 676 for the southern chaparral areas, 668 for the deserts, 589 for the mountain forests of California, thence diminishing to 129 for the coastal strip.

Other xeric warm temperate areas such as central Chile and Argentina, much of Australia, and western parts of southern Africa also possess large bee faunas, although to judge by the taxonomic literature and collecting impressions, they are smaller than those cited in the preceding paragraphs. Unfortunately there are few faunal data for these areas. There is a species list for Mendoza, Argentina (Jörgensen, 1912), as shown in Table 1. Moldenke (1976b) has compared the faunas of the temperate coastal areas of Chile and the western United States. For the climatically Mediterranean area of Chile and for the deserts he reports 183 and 176 species respectively, while comparable figures for California are 676 (for the southern part of the Californian Mediterranean area only) and 668 (for the Californian deserts). The full meaning of these numbers is not clear, in part because of the problem indicated in the footnote to Table 1, and in part because of the less intense collecting in Chile than in California. Moldenke, however, believes the differences in number of species between comparable Californian and Chilean areas to be real, and I see no reason to disagree with him.

In mesic temperate areas such as the eastern United States or central Europe, the numbers of individuals and species are markedly less than in the xeric regions of the same continents. Local lists generally have fewer than 300 species, exceptions mostly being those for more southern localities or large areas. One of the most carefully collected localities in the world must be Carlinville, Illinois, where Robertson found 297 species. The large number of species (566) reported for Germany might cause one to question the view that central Europe has a smaller fauna than that of the Mediterrean, but it must be remembered that Germany is a moderately large and diverse area that has been meticulously collected in many localities by a large number of specialist collectors of bees. Such careful collecting has never been done in any Mediterranean area.

As indicated in Table 1, bee faunas decrease rapidly as one approaches and enters the Arctic, in spite of the abundance of flowers in arctic habitats.

The few data from the tropics in Table 1 appear to support the view that tropical bee faunas are not as large as those of some temperate xeric and mesic areas. The local fauna of Barrackpore in Bengal was sampled by a person interested in bees and wasps over several years and yielded only 73 species. There is no way to judge the intensity of the collecting, however. The fauna of Java, about 193 species, should be viewed in the perspective that it has been studied by persons having special interests in bees and that Java is a large, altitudinally diverse island that was connected with Asia so recently that it has a rich Oriental fauna, not a specialized insular fauna.

My impressions of the African tropics, in the absence of appropriate data, are that the bee fauna is richer than that of the Oriental tropics. The American tropics are richer still. Thus Panama has a smaller area than Java, but a much larger known bee fauna, and certainly many species yet to be discovered. Indeed the

the vicinity of Belém do Pará, Brazil, a low, flat region, has a much larger fauna than the whole of Java with all of its diversity. My own observations, supported strongly by those of Dr. J. van der Vecht (in litt.) who has worked both in Indonesia and Surinam, are that flowers attractive to bees are far more abundant and diverse in and at the edges of forests in the Neotropical than in the Paleotropical regions. Presumably the bees and flowers coevolved. It is not clear why such a regional difference should exist. The important point is that, although data from the tropics are meager, Table 1 and collecting impressions both clearly show that there is no great abundance of species (or genera) in the tropics as compared to temperate regions.

There are various possible explanations for the abundance of bees in some xeric areas and their scarcity, relative to what would be expected from experience with other organisms, in the tropics. Most bees, like the sphecoid wasps, store their highly perishable larval food (for bees, pollen mixed with nectar) in cells excavated in the soil and only thinly lined with secreted waxy or cellophanelike material. In humid environments the loss from fungal attacks on such food and on immature bees is substantial and sometimes catastrophic. Dr. J. G. Rozen has suggested (in litt.) that another problem for bees in humid areas may be hygroscopic liquification of the food provided for their larvae, which therefore drown. As noted below, the bee groups that are most successful in humid areas are mostly those of that no longer nest in the soil, or that do not use simple cells excavated in it. An unusual case of larvae in excavated cells in the tropics surviving for months below the water table is that of *Epicharis zonata* which lines and seals its cells with thick resinous material (Roubik & Michener, in press). Even larvae in the rather simple cells of Andrenidae and Halictidae may survive flooding for a few days (Michener, personal observations). Nonetheless, most bees do not live under such conditions and the disjunct southern distribution of certain primitive groups of bees, as described in the subsequent sections, is consistent with an origin of bees in xeric parts of Gondwanaland.

Another reason for the moderate size of the bee faunas in the humid tropics may be the success of a few kinds of highly social bees there, as suggested by D. W. Roubik (in litt.). The genus *Apis* is represented by three of four species in southeast Asia, one species in Africa, and was until recently absent in the Americas, while the other highly social bees (Meliponinae) are most abundant in the Americas. Each such species may be, from the standpoint of floral resources, the ecological equivalent of a number of species of nonsocial bees, for the highly social species are active all year and are generalists while the nonsocial species are often seasonal. Indeed, it is possible that each of the highly polylectic *Apis* species is the equivalent of several meliponines and many solitary species. Competition from aggressive generalists could have an important influence on the tropical faunas.

Table 2 summarizes, in part subjectively, the relative abundance and diversity of bees in various climatic and geographical areas. Of course, much depends on the particular areas compared, for the local soil, floral conditions, temperature, and other factors play a major role.

It seems that some of the world's warm temperate, xeric areas are, for bees,

TABLE 2. Relative abundance and diversity of bees in various areas, from most abundant (1) to least abundant (10).

1.	Warm temperate xeric (Madrean, Mediterranean to Central Asia)
2.	Temperate mesic
3.	Moist tropical (American)
4.	Other warm temperate xeric areas (S. Africa, Australia, Chile, etc.)
5.	Temperate prairie, steppe
6.	Moist tropical (Old World)
7.	Tropical grasslands and savanna
8.	Cool temperate xeric
9.	Extreme deserts
10.	Frigid areas

what the tropics are for many other groups. That is, these areas are centers of diversity, of evolution, perhaps areas of origin for various taxa, and reservoirs for taxa which have never extended more widely or have retreated to and survived in these xeric areas. A problem with this concept is that the dry areas of the world are not necessarily ancient. For example, those of North and South America probably date only to the Pliocene. As will be suggested below, bees very likely arose in dry areas and have radiated to a major degree in such areas. Groups actually restricted to them probably spread by long distance dispersal. (Shorter distances sufficed in dry epochs or between edaphically dry areas.) Moreover, mesic-adapted taxa probably entered and proliferated in dry zones. Thus when a dry region arose, it could be populated by a bee fauna that often became larger than that of adjacent mesic regions.

Mere aridity, however, does not assure a large bee fauna. Mediterranean climates (winter wet season, warm dry summers, macchia or chaparral vegetation) have rich faunas, as exemplified by parts of California and the Mediterranean basin. So also do still more xeric warm regions with regular but small rainfall, characterized by extensive development of succulent vegetation such as cacti, African *Euphorbia*, and Aizoaceae. Thus the desertic region (Sonoran and Chihuahuan) of the southwestern United States and northern Mexico has a large bee fauna, both in those parts (west of about 113° W) where the rainfall is principally in winter and in those where it is in summer. The contrast is striking with areas in the same latitude but with a mesic climate, such as the eastern United States. Cool desertic areas, like the northern part of the Great Basin of North America or much of Patagonia, also do not have especially large bee faunas.

Interestingly enough, the contrast is also striking with tropical and subtropical xeric areas. For example, there is no evidence of an enriched bee fauna along the the southern edge of the Sahara, in spite of the proximity of a very rich Mediterranean fauna in North Africa, and in spite of climatically habitable areas that must have joined these zones in various places in relatively recent, more humid times. Also, there is no evidence of faunal richness compared to nearby areas in several other dry regions in or near the tropical zone. Thus northeastern Brazil, northern Australia, northwestern India and western Pakistan, so far as known, have poor faunas compared to other parts of the same continents. Tropical savannas such as those of east Africa, Venezuela, Panama (Michener, 1954), and northern Queensland also have poor faunas, and the drier tropical areas are in

effect depauperate savannas. To the bee collector, arid tropical areas appear to have much less flowering throughout the year and less synchronization of flowering than the warm temperate, dry areas.

Warm temperate grasslands (prairie or steppe), especially the more mesic or cooler ones, have moderate bee faunas, becoming rich where the grasslands are arid and interspersed with xeric vegetation like that of the Sonoran and Chihuahuan deserts. Bee faunas of temperate grasslands are substantially larger than are those of tropical grasslands and savannas. Prairies have conspicuous flowering seasons with many kinds of flowers, in contrast to many tropical savannas. In South America there is more or less continuous savanna and grassland from central Brazil to the Argentina pampa, with the bee fauna seeming to become richer as one progresses southward, and probably becoming richer still in the desertic parts of central Argentina, which resemble the Sonoran region in vegetational aspect.

There are, of course, certain groups of bees that are not most abundant and diversified in the xeric warm temperate areas. The principal such groups are the following:

Hylaeinae: Most abundant and diversified in mesic or humid areas, temperate and tropical. Scarce in desertic areas, perhaps because of scarcity of pithy stems which are the favored nesting sites.

Ceratinini: The same comments apply except that this tribe is not much diversified in the temperate areas of the Northern Hemisphere.

American Halictinae: Most common in temperate and tropical mesic or even humid areas, usually scarce in xeric areas except in limited mesic environments therein. In the Palearctic region, however, various halictines (e.g., *Halictus* s. str., *Vestitohalictus*, *Nomioides*) are abundant, with many species in Mediterranean and similar climates.

Andreninae, Macropodinae, the genus *Nomada*, Bombini: Most common in mesic temperate, even cool temperate, areas; distinctly less common or almost absent in desertic as well as tropical regions.

Nomiinae, Ctenoplectrinae, Xylocopini, Tetrapediini, Centridini, Cteniosche-lini, Rathymini, Meliponinae, Apinae, Euglossini: Best developed in tropical, mostly moist tropical, habitats. These groups (except Nomiinae) occur commonly in forested regions and mostly nest in wood, in preformed cavities of various sorts, in termite nests, or line their cells with resin or wax (Centridini) or are parasites in nests of Centridini. Thus except for Nomiinae and some Centridini, they do not construct nests in soil like most solitary bees and are therefore presumably less subject than most to damage to food and immature stages by moisture and fungi. [Several other groups (e.g., Augochlorini among American Halictinae; Exomalopsini) have many genera and species in moist tropical regions even though they are most abundant outside of such areas.]

Most groups of bees other than those listed above are either as abundant and diversified in warm temperate xeric areas as elsewhere, or are more so. More details, together with bibliographic references, are given in the section on Distributions of the Groups of Bees.

Origin and Antiquity of Bees

There is no doubt, on morphological grounds, that bees arose from the sphecoid wasps. There is no evidence that any extant sphecoid group is most closely related to bees, or is ancestral to them; the bees and sphecoid wasps probably had a common ancestor that had wasplike feeding habits and that would be considered a sphecoid wasp if it were known to us. It is clear that a shift from animal food to pollen as the principal protein source was the major event in the origin of bees. Indeed, the bees are probably best regarded as a part of the Sphecoidea rather than as a separate group of the Hymenoptera (Brothers, 1975).

All bees are dependent on products of angiosperm flowers (nectar, pollen, sometimes oil) for food. The group therefore must have arisen at the same time as or after the angiosperms. Various authors (e.g., Baker & Hurd, 1968) have noted that the more primitive groups of angiosperms (e.g., Magnoliaceae) are largely pollinated by beetles. Hence it seems likely that bees arose or at least became common with the subsequent evolution of angiosperms. In their excellent review of angiosperm biogeography, Raven & Axelrod (1974) indicate that angiosperm fossils first appear in middle Lower Cretaceous, that by early Upper Cretaceous angiosperm pollen is becoming more abundant than spores of ferns and pollen of gymnosperms, and that by the end of the Cretaceous there was much diversity among angiosperms. Some forms present at that time (e.g., Myrtaceae, *Ilex*) are in families and genera now visited extensively by bees, and it is probable that bees were present and perhaps abundant by that time (Maastrichtian, 65–70 m.y. BP).

The earliest known fossil bees are from the late Eocene Baltic amber (see review by Zeuner & Manning, 1976, and for Meliponinae, by Wille, 1977). That fauna includes diverse groups of bees, including long-tongued families, especially the Apidae. It is obvious that the bees had already evolved for some time before the late Eocene.

It is probable that bees arose in the Upper Cretaceous. The complete absence of unusual archaic bees from New Zealand and New Caledonia, however, might suggest that there were few or no bees in Gondwanaland when these areas were isolated 60 to 80 m.y. BP (Smith & Briden, 1977), after the middle of the Upper Cretaceous, by the splitting of that continent. A more likely explanation is that bees were scarce in the moist temperate forests of these islands and eastern Australia when the split occurred (Raven & Axelrod, 1972); they may have been better represented in other places and any that were on these islands may have been exterminated during the long subsequent history of changing climates and sea levels.

Except for fossils in amber, wings are often the only well-preserved fossil structures. Unfortunately, while wings often contain many useful characters, they may not indicate the family to which a bee belongs. Relations of species not assignable to modern genera are therefore highly suspect, especially when published by persons who were not bee specialists. The following list indicates the earliest records that, from the literature, seem probably accurate, for various groups of bees:

Halictinae—Oligocene (Colorado)
Andreninae (*Andrena*)—Eocene (Baltic Amber)
?Ctenoplectrinae—Eocene (Baltic Amber)
Melittinae (*Melitta*)—Oligocene (Colorado)
Anthidiini—Oligocene (Colorado)
Megachilini—Oligocene (Colorado)
Xylocopini—Miocene (perhaps Oligocene) (Europe)
Anthophorini—Oligocene (Colorado)
Meliponinae—Eocene (Baltic Amber)
Bombini—Oligocene (Colorado)
Apini
(*Electrapis*)—Eocene (Baltic Amber)
(*Apis*)—Oligocene (Europe)

Speculations as to antiquity of various groups, based on distributional considerations, will be included in subsequent sections. The only use for the above list is to indicate minimum ages of groups. Not a single fossil bee (except some Pleistocene or Recent *Trigona* assigned to extant species) has been found in the southern continents. The fossil record, in short, is so poor as to have almost no biogeographical significance (except in the genus *Trigona*).

The presence of long-tongued Apidae (forms with mouthparts much modified as compared to wasps) in the Eocene suggests rapid early radiation. It is likely that most bee families were recognizable in the Eocene and quite possibly before. One of the problems in understanding bee evolution is how so much of the evolution of the group could have occurred in the perhaps 20 to 30 m.y. from the appearance of probably bee-pollinated plants (taxa now visited by bees) in the latest Cretaceous (Maastrichtian) until the Eocene when fossils show the presence of the presumably most derived family, Apidae. Major morphological reorganizations, particularly of the mouthparts, are involved. As will be noted in subsequent sections, biogeographic evidence suggests an earlier origin for bees than the Maastrichtian. Much of the reliable evidence of times of appearance of angiosperm groups is based on fossil pollens (Muller, 1970). Before late Cretaceous, most of the pollen is unidentifiable as belonging to any modern group of plants. It is therefore likely that early bees utilized some of these pollens and that one need not delay the origin of bees until appearance of known bee-pollinated plants. Such plants, moreover, tend to produce limited quantities of sticky pollen that does not blow extensively in the wind. It may be, therefore, that bee-pollinated plants became abundant, especially in dry areas, well before their pollens appeared in the fossil record. For those reasons one can postulate that bees arose earilier, let us say, by mid-Cretaceous. This would have allowed them 60 m.y. of evolution before their first fossil appearance and their early radiation could have been relatively gradual.

The place of origin of bees remains obscure but one can speculate both as to the place and its climate. The xeric interior of the old continent of Gondwanaland, particularly West Gondwanaland (Africa-South America), has been suggested as the area of origin of angiosperms (Raven & Axelrod, 1974). It presum-

ably had a seasonal temperate climate. Xeric regions, especially those with sandy soils, are commonly areas of abundance for sphecoid wasps, most of which nest in the ground. It is not unlikely that bees arose from these wasps in such a place. If so, they have retained their association with xeric areas and have been, compared to the angiosperms, relatively unsuccessful in adapting to humid climates. Possible reasons for this have been discussed previously in the section on Areas of Diversity and Abundance.

Dispersal of Bees

Because bees fly well, one might think that they would be rather successful at crossing barriers, such as water or areas that are climatically or vegetationally inhospitable. A female bee usually mates early in adult life and carries enough sperm cells alive in her spermatheca to last for part or all of her reproductive life. One can therefore assume that, except for the few highly social bees (Meliponinae, Apinae) that must swarm as a communicating group to establish new colonies, an individual female transported across a barrier might be able to nest, reproduce, and thus establish a population. If she carried sperm from several males, as is likely for many species, the genetic limitations of such a new population would not be so severe as if she had mated only once. The ability of a bee in a new area to fly about and perhaps find suitable nest sites and food sources also would seem to enhance the probability of establishment.

Nonetheless, distributional data suggest that most groups of bees are not particularly good at crossing major barriers. Most bees fly only in good weather so that they are likely to be in their nests during storm winds. Moreover, not only individuals but successive generations of solitary to primitively social species commonly return to the same nesting site, so that they tend to be quite sedentary (Michener, 1974).

Michener (1953) noted, for *Megachile brevis*, that when favored flowers in an area wilted, bees left, and appeared and continued nesting in other areas. One marked female appeared 8.8 km from the site where it had been nesting. Moreover, E. G. Linsley (in litt.), discussing the spotty blooming of desert flowers in response to spotty rainfall, notes that in 1959 large numbers of females of *Andrena linsleyi* dug burrows near a small patch of the host flower, *Oenothera deltoides*, most of the bees, perhaps, having migrated from surrounding sites now with few flowers but where the *Oenothera* bloomed profusely in the two preceding years. The nearest such site was 3.2 km distant. Such dispersal is unusual, however. For most solitary or primitively social bees, while some individuals must disperse, and of course new nesting sites do develop, the majority of individuals seem to remain at established sites. If conditions are bad, the population diminishes, seemingly not because of dispersal but because of death or failure to reproduce.

Thus for the majority of kinds of bees, dispersal has been by slow spread across continents or to nearby land masses, or by transport on moving continents. The Antillean and central Indonesian faunas, however, show that scattered islands between continents can serve as stepping stones for many taxa.

There is some evidence that solitary to primitively social bees that nest in wood

or stems are more likely to cross moderate water gaps than are those that nest in the ground. Thus a large percentage of the long-tongued (relatively derived) genera of bees in Australia belong to groups such as Lithurginae, Megachilini, and Xylocopinae that commonly nest in stems or wood (Michener, 1965a). The same groups are a major part (although by no means the only components) of the Indo-Australian tropical fauna that extends from India to Southeast Asia, Indonesia, and in diminishing numbers to the Solomon Islands and northern Australia. Many water gaps existed in this region even in times of lowered sea levels, yet some species are very wide ranging in it, showing repeated, relatively recent, successful crossing of water. Perhaps wood or stems are rafted or blown in severe storms often enough to account for the higher frequency of such distributions in these bees than in ground-nesting forms.

When one examines the bee faunas of oceanic islands, it becomes apparent that dispersal across water favors minute forms in addition to the moderate-sized to large, wood-nesting species. For example, on the oceanic islands of the Pacific (Fiji, Samoa, Hawaii, Micronesia, etc.) there are a few moderate-sized, wood-nesting *Lithurge* and *Megachile*, perhaps carried to some of the islands by Polynesians. Otherwise the fauna consists largely of small ground-nesting *Homalictus* (Halictini) or of *Hylaeus*; the latter are also small bees but they nest in wood, in stems, or in holes in rocks or soil. It is only among the small forms, especially *Hylaeus* in Hawaii (Perkins & Forel, 1899) and *Homalictus-Echthralictus* in Samoa (Michener, 1978a), that there has been significant evolution in these isolated oceanic islands. Thus it seems that dispersal, presumably by wind at least for *Homalictus*, must have favored small forms, while the larger ones probably came later and perhaps in some cases with the help of man. The New Zealand fauna, however, consists largely of middle-sized ground-nesting *Leioproctus* from Australia, and the Galapagos Islands lack small bees and have only one large form, the wood-nesting *Xylocopa darwini*, which belongs to a tropical American subgenus. The presence on the Galapagos of the large meloid parasite (*Cissites*) of *Xylocopa* suggests arrival of the bee from the mainland in a floating log (E. G. Linsley, in litt.) although the female bees are powerful fliers and have been seen far out to sea among the islands (Linsley, in litt.; Cheesman, 1929).

Less isolated island groups frequently have larger faunas, including small as well as larger bees, both those that nest in soil and those that nest in wood. For example, the rather large megachilid *Creightoniella frontalis* (and its subspecies or allied species *C. atrata*) ranges for 6,400 km from Sumatra to the Solomon Islands; this is a ground-nesting species, and presumably the adults have flown or been blown across the water gaps. The Antillean fauna has probably all or nearly all arrived across the water. Yet it includes not only bees that nest in wood and minute bees, but also moderate-sized to large ground-nesting bees such as *Caupolicana*, *Melissodes*, *Anthophora*, *Agapostemon*, etc. (Alayo Dolmau, 1973). They probably were blown from Yucatán or elsewhere by hurricanes or other storms.

The highly social bees (Meliponinae, Apinae) present special biogeographical problems. They disperse by swarming or by absconding as colonies, not by individuals, most of which in any case are nonreproductive workers. In Meliponinae, a new colony is established by individuals from the parent colony which go

back and forth provisioning the new nest, before a queen goes there. Thus dispersal by flight across even a few hundred meters of water would be impossible, a view supported by the apparent isolation of some species or subspecies by Brazilian rivers (J. S. Moure, verbal communication). The absence of Meliponinae from the Antilles (except for one species probably introduced by primitive man), in spite of their abundance on the mainland, supports this view, although there is a fossil *Trigona* from Hispaniola. The presence of Meliponinae through the East Indies and as far east as the Solomon Islands, however, suggests other means of dispersal. In Apinae dispersal is by swarms or migrating colonies which may fly for distances of perhaps dozens of kilometers, or across habitable country where they can stop, hundreds of kilometers. Yet traversal of a broad ocean by an organized swarm would be impossible. There are three mainland *Apis* species in the Philippines, but the water gaps were much narrower or absent when the sea level was lowered in the glacial periods.

In view of the distribution of Meliponinae in the East Indies, these bees must rarely cross substantial water barriers as colonies in natural rafts or perhaps even in hollow logs floating in the sea. They store food supplies, and those that inhabit hollow logs often close entrances with waterproof resin under unfavorable conditions, and therefore might survive weeks of drifting. Nests of *Melipona compressipes manaosensis* in the Amazonian riparian forests survive long annual periods of submergence in river waters (Kerr, 1969). The presence of *Apis* east of Wallace's Line in Indonesia (*A. dorsata* as far east as Timor) may be explained similarly. However, migrating swarms of *Apis* may occasionally cross water gaps like those among the Indonesian islands, or at least the narrower ones of the glacial periods.

Floral Relationship

This section is not a comprehensive treatment of floral relationships of bees. It concerns only those topics having direct relationship to geographical distribution, and cites only certain examples, among many that are known, of the relationships described.

Bees vary widely in their floral requirements. Most will take nectar from a variety of kinds of flowers. Hence male bees and females that are not collecting pollen are not usually very specific in their flower visiting habits. Some species likewise collect pollen from many different and unrelated kinds of flowers. Such bees are called *broadly polylectic* (supergeneralists of Moldenke, 1975). Other species restrict pollen collecting to a few related flowers, commonly in the same genus (or even to a single species) and are called *oligolectic* (or *monolectic*). These are the superspecialists of Moldenke (1975). Presumably the majority of bees collect pollen from several kinds of flowers (not necessarily closely related) in most of the communities that they inhabit, often from different flowers in different communities or at different seasons. Such forms are called oligolectic by Moldenke (1975) but this is contrary to the usual use of the word. The expression *narrowly polylectic* seems in accordance with common usage for such forms. All intergradations exist between broadly polylectic species (such as *Apis melli-*

fera) and oligolectic or monolectic species. The distinction that is most often confusing is between oligolectic and narrowly polylectic, and there will always be differences of opinion for some species. However, if a bee collects pollen only or very largely from a few related species of a genus or family of plants, it is oligolectic, whereas if it collects from unrelated plants (e.g., like some *Osmia* of the subgenus *Nothosmia*, from *Phacelia*, Hydrophyllaceae; certain species of *Penstemon*, Scrophulariaceae; and perhaps a few Leguminosae), I would call it narrowly polylectic, even if only a few floral species are involved. This usage is in accordance with that of Robertson (1899), Malyshev (1936), and others, often using the root—trophic rather than—lectic. There is no need to discuss here the morphological interrelations that sometimes are obvious between oligolectic bees and their favored flowers, nor the attributes of the flowers visited by a bee species that utilizes several kind of flowers. In the present context, the important point is to determine the possible influence of the distributions and abundance of flowers on the distributions of bees.

Obviously bee faunas and the floras of flowering plants with which they are associated are interdependent. Yet there is no close relationship between the numbers of species in each. Thus the moderate-sized floras of the Galapagos Islands and Iceland are associated with only a single polylectic bee species each, *Xylocopa darwini* on the Galapagos and *Bombus jonellus* on Iceland. Moreover, the very rich tropical floras are associated with only moderate-sized bee faunas. The same inconsistencies are found on more local levels. For example, the extraordinarily rich flora of the Cape region of South Africa is associated with a moderate-sized bee fauna, and it is my impression from collecting experiences that as one goes inland from the Cape area, away from the windy, often cool, coastal zone, into a less rich floral region, the bee fauna does not become smaller and may in fact become larger.

Floral richness of bee-pollinated plants, such as occurs in the tropics, associated with only moderate bees faunas, is possible because of generalist bees that pollinate many species of plants. In the tropics the outstanding polylectic bees are the highly eusocial *Apis* and Meliponinae, all species of which are active throughout the year and thus not seasonal like flowering of most plants. The Halictinae are another major taxon, abundant in the tropics, most species of which are polylectic.

In an earlier paper (Michener, 1954) I noted geographical variations in the relative abundance of oligolectic species of bees. In the Western Hemisphere the highest percentages of oligoleges are found in the bee fauna of xeric regions like the Sonoran, perhaps lower percentages in prairie areas, certainly lower in mesic eastern North America, and lowest in the moist tropics. Moldenke (1975, 1976a, 1976b) found 60 to 62% of the bee species in California to be oligolectic in different Sonoran desert areas, 50% in the high mountains, 40–50% in Californian areas of Mediterranean climate, and 30% in the coastal strip. Robertson (1929b) found 28% of the species oligolectic in southern Illinois; this figure is high because he studied only a limited area and some of his "oligoleges" are narrowly polylectic when viewed from a broader standpoint. By contrast, a recent year-long study in French Guiana by D. Roubik and the author revealed only one or two percent of the total that were clearly oligolectic in this moist tropical area. Of course, various

uncommon species were collected on only one flower species in the course of a year's collecting. Thus larger numbers of oligoleges could exist but the percentage seemed clearly low.

In 1954 I suggested that in the xeric areas, where flowering tends to be synchronized and where many kinds of bees therefore have overlapping short seasons of flight, so that seasonal segregation is impossible, there are advantages in oligolecty, which divides available food resources (probably limiting in some years) among species and reduces interspecific competition for those resources. In the tropics, at the other extreme of the series, many species of bees have long seasons of flight or are active throughout the year, and the plants' flowering periods are scattered and sometimes long. There is no season without flowers. The abundance of individual bees at any given time is usually much less than at the season of major flight in the Sonoran or Chihuahuan deserts. Most flower species in the tropics are not in bloom for as long as the flight periods of most bees, so that oligolecty is often impractical. Areas like the eastern United States are intermediate, with a long period (e.g., March to September) when bees are active, different species flying at different seasons. With such seasonal segragetion, even rather broadly polylectic bees are often prevented from competing, and there is thus less pressure than in the deserts for oligolecty as a device to partition resources.

These ideas seem compatible with Moldenke's (1976b) conclusions that in California, areas with the largest bee faunas have the highest percentage of oligolecty, and those with the fewest species of bees have the lowest percentage of oligolecty (my definition of the term). We seemingly agree that the larger the number of species that is in flight during the same season of the year, the higher the percentage of oligolectic species.

It is not clear whether information from outside of the Americas supports these hypotheses and interpretations. We need data on such matters as the following: Is the percentage of oligolectic bee species higher in the Mediterranean basin than in central Europe? Is the percentage of oligolectic bee species higher in western South Africa than in equatorial Africa? (My subjective answer to the last question, based on a few months' collecting in each area, is *yes*.)

A reasonable criticism of the ideas presented above is that the high frequency of oligolecty in the xeric, warm temperate areas has been documented only for the Western Hemisphere and is due largely to Panurginae. Since most panurgines are oligolectic, and since they are especially numerous in the xeric warm temperate areas of the Western Hemisphere and particularly scarce in the tropics, their mere existence might lead to the described geographical variation in percentage of oligoleges in the bee fauna. If one eliminates the Panurginae, however, there are still high percentages of oligolecty in the western United States compared to the East, and the low percentage in the tropics remains unchanged.

The distribution of an oligolectic bee may on occasion be limited by the distribution of its pollen source. For example, before its dispersal by man, the genus *Cucurbita* was probably not found east of a line through east Texas and central Kansas, except for a species in Florida. Man dispersed *Cucurbita* as a crop plant, and now one species of *Peponapis* and two of *Xenoglossa*, oligolectic bees on this plant, range to the Atlantic coast, the *Peponapis* reaching New England (Hurd &

Linsley, 1964). Apparently the bees had the potential to withstand the climate far beyond the natural range of their host plant, for they have now expanded their ranges by half the width of the continent. There is no evidence that the plant is limited by its oligoleges. Where it is introduced in the absence of its oligoleges, polylectic bees provide pollination.

Similar examples on a smaller scale are not uncommon. Thus *Prochelostoma philadelphi*, an oligolege on *Phildalephus*, occurs in gardens well beyond the range of native plants of this genus, for example, in Lawrence, Kansas. This is some 300 km northwest of the natural range of *Philadelphus*.

Very often, plants extend beyond the ranges of their oligolectic bees and also occur, within the general ranges of the bees, in local populations lacking such bees. For example, the boraginaceous genus *Cryptantha* ranges widely over the western United States, east to Kansas, and south in Mexico and into South America. A few species of the genus *Andrena* and all species of the megachilid subgenus *Proteriades* and its close relatives have short, hairy mouthparts morphologically adapted to extract pollen from the very small flowers of *Cryptantha*, and are usually considered as oligolectic visitors of *Cryptantha* (Timberlake & Michener, 1950). [In spite of what appear to be clear morphological adaptations for collecting pollen of *Cryptantha*, however, some species of *Proteriades* at some times (perhaps when *Cryptantha* is scarce) use pollen from other sources in provisioning their cells (Parker, 1978). It may be that most oligolecty breaks down on occasion.] These *Cryptantha* oligoleges are primarily Californian, although some *Proteriades* range, as rare, localized populations, as far east as the Dakotas and New Mexico. It is obvious that the plant can get along with general (polylectic) pollinators and is not dependent upon oligoleges. As noted by Linsley et al. (1973), bee pollination frequently has played only a minor role in plant evolution despite specialization and oligolecty of some of the bees. Even when there appears to have been coevolution of plant and bee as in some species of *Clarkia* and its oligoleges, there appear to be populations of the plants without the oligolectic visitors but pollinated by polyleges (MacSwain et al., 1973).

Another illustration of the same thing can be deduced from the *Larrea divaricata-tridentata* species pair, an amphitropical bush found in deserts of both North and South America. In both continents it has oligolectic (in North America, monolectic) bee visitors, but they belong to different genera in the two hemispheres. For example, various oligolectic species of *Perdita*, *Nomadopsis*, *Ancylandrena*, *Megandrena*, *Hesperapis*, *Emphoropsis*, *Heteranthidium*, and *Hoplitis* visit flowers of North American *Larrea* (Hurd & Linsley, 1975), but these genera do not occur in South America. Other species of *Larrea* are all South American, and it seems likely that the genus jumped across the tropics in geologically very recent times to become established in Mexico and the southwestern United States. It could not have come with its South American oligoleges. Therefore it must have survived in North America for a long time, being pollinated by the general pollinators (polyleges), before its North American oligoleges evolved.

Sometimes oligolectic bees appear to play no role in pollination of their host plants. An example is *Perdita wootonae*, an oligolectic visitor to flowers of *Mentzelia decapetala*. It flies only in the late afternoon when the *Mentzelia* flowers

open. The tiny bees climb out on the long radiating stamens and collect pollen individually from the anthers, and do not usually even approach the stigma (personal observations). They are thus in effect parasites. The whitish flowers are normally pollinated by sphingid moths. Similar observations have been made for *Perdita texana* on flowers of *Opuntia* (Barrows et al., 1976).

From accounts such as the above, one can conclude that sometimes the distribution of a bee species or genus is dependent upon the presence of a particular flower (as in *Peponapis* and *Xenoglossa* on *Cucurbita*). The general distributional limits of the oligolectic bees, and of course also polylectic bees, ordinarily result from climatic factors, barriers to dispersal, and presumably competition with other bees for food or nest sites, not from lack of specific food plants. Plants commonly range more widely than their oligolectic visitors and thus are not dependent upon the latter for pollination. Even outcrossing plant species that have oligoleges commonly reproduce quite well without the oligolectic visitors, thanks to polylectic pollinators.

Distributions of the Groups of Bees

In this section the distributional patterns of each group of bees are discussed, and explanatory comments are included where they seem useful. In view of Raven & Axelrod's (1974) treatment of continental movements and associated climatic changes in relation to angiosperm biogeography, I have not repeated information on such movements but have used their summary in attempting to explain, in this and the next section, certain historical aspects of apoid biogeography.

In the following account and in Table 3, I have used certain terms that require explanation for geographical areas. Because bees are so well developed in some of the world's arid areas, these have been segregated and are repeatedly referred to. The abbreviations used for the columns of Table 3 are listed below:

1. Australia (Ast). In Table 3 the following area (2) is segregated. Tasmania is part of the same faunal area but is mentioned separately in the text.

2. Northern Australia and New Guinea (NAt/NG). The northern extremity of Australia, especially where forested, and New Guinea, Bismarck Archipelago, and nearby islands.

3. New Zealand (NZ).

4. Oriental region (Ort). Tropical Asia from Sri Lanka (Ceylon) and the lowlands of India to Viet Nam and southeasternmost China, also Indonesia (except New Guinea) and the Philippines, although these are mentioned separately in the discussion.

5. Madagascar (Mdg).

6. Africa (Afr). Subsaharan Africa except as indicated below (7). Note that Africa as used in the text does not include the north coast of the continent. In Table 3 it also does not include the Cape region.

7. Cape region of Africa (Cpe). The area of Mediterranean climate with Cape macchia plus the more desertic Karoo and the Namib Desert area.

TABLE 3. Summary of distributions of tribes, subfamilies and families of bees. Areas (column headings) are listed in the text. The number of + signs in any row indicate the relative abundance and diversity of that taxon in different areas; comparison of the number of plus signs for various taxa up and down a column is of no value. m = entering an area only marginally, or one species extending well into an area but not half way across it.

	Ast	NAt/ NG	NZ	Ort	Mdg	Afr	Cpe	Pal/ arc	Med/ CA	Ne/ arc	Mad	Neo/ tro	Ant	Arg/ Brz	Ara
Euryglossinae	++														
Hylaeinae	+++	++	+	+	+	+	+	++	+	+	+	+		+	
Xeromelissinae										m		+		+	++
Paracolletini	+++	+	+			m	+				+	+		++	++
Colletini						+	+	+	+	+	+	+	+	+	+
Diphaglossinae										m	+	+	+	+	+
Stenotritinae	+														
Oxaeidae										m	+	+		+	
Dufoureinae				+		+	+	+	+	++	+				+
Nomioidini	+	+		+	+	+	+	+	+						
Augochlorini										+	+	+++	+	++	+
Halictini	++	+	+	+	+	++	++	+++	+++	+++	++	+	+	+	+
Nomiinae	++	+		++	++	+++	+	+	+	+	+		+		
Andreninae						+	+	+++	++	+++	++	m			+
Panurginae					+	+	+	+	+	+++	+++	+		++	++
Macropodinae								+	+	+					
Ctenoplectrinae		+		+		++		m							
Melittinae						+	++	+	+	+	+				
Dasypodinae							++	+	+	m	+				
Fideliidae							+								+
Lithurginae	+	+		+	+	+	+	+	+	+	+	+	+	++	++
Megachilini	++	+		+	+	++	+	++	++	++	++	++	+	++	+
Anthidiini		m		+	+	++	++	+	++	+	+	+	+	+	+
Dioxini							+	+	++	+	+				
Xylocopini	+	+		++	+	++	+	+	+	+	+	++	+	+	m
Ceratinini	m	+		++	+	+++	+	+	+	+	+	++	+	+	+
Exomalopsini-Ancylini				m					+	+	+	++	+	+++	+
Pararhophitini									+						
Tetrapediini												+			

TABLE 3. *Continued.*

	Ast	NAt/ NG	NZ	Ort	Mdg	Afr	Cpe	Pal/ arc	Med/ CA	Ne/ arc	Mad	Neo/ tro	Ant	Arg/ Brz	Ara
Melitomini										+	+	+		+	+
Eucerinodini															+
Canephorulini														+	
Eucerini				+	+	+	+	+	+	++	++	++	+	+++	++
Anthophorini	+	+		++	+	++	+	++	+++	++	++	+	+	+	+
Melectini	+	+		+		+	+	+	++	+	+		+		
Centridini										m	+	++	+	+	+
Ctenioschelini										m	+	++	+	+	+
Rathymini												+			
Nomadini	m	+		+		+	+	++	+	++	++	++	+	++	+
Epeoloidini								+		+					
Protepeolini											+	+		+	
Isepeolini														+	+
Caenoprosopidini														+	
Neolarrini										+	+				
Townsendiellini											+				
Ammobatini					+	+	++	+	++	+	+				
Holcopasitini								+	+	+	+				
Biastini								+	+		+				
Ammobatoidini								+	+						
Meliponinae	+	+		++	+	++						+++		++	
Euglossini												++	+	+	
Bombini				+				+++	+	++	+	+		+	+
Apinae				++	+	+	+	+	+						
Total taxa	15	15	3	18	15	23	23	29	29	33	34	28	17	27	24

8. Palearctic region (Pal/arc). The palearctic faunal region. In Table 3 the following area (9) is excluded from the Palearctic.

9. Mediterranean Basin through Asia Minor to desertic areas of Central Asia (Med/CA). Includes the Canary Islands, Azores, etc.

10. Nearctic region (Ne/arc). The Nearctic faunal region. In Table 3 the following area (11) is excluded from the Nearctic.

11. Madrean region (Mad). The areas of California having a Mediterranean climate, mostly with macchia or chaparral (Californian), plus the more desertic areas from southern California to west Texas and south through the Mexican plateau. This includes the Chihuahuan and Sonoran deserts. The term Madrean is derived from the works of Axelrod (e.g., 1958).

12. Neotropical region (Neo/tro). The Neotropical faunal region, from tropical Mexico southward. In Table 3 the regions listed below (13–16) are all excluded from the Neotropical.

13. Antilles (Ant). The Greater Antilles, except when the Lesser Antilles are specifically mentioned.

14. Temperate South America. The next two regions (15, 16) together.

15. Argentina-southern Brazilian area (Arg/Brz). The area of temperate Brazil and adjacent countries, south into Argentina, including the central desertic parts of Argentina.

16. Araucanian region (Ara). Chile and the adjacent parts of southern Argentina (Ringuelet, 1961).

The data in the following more detailed verbal account are summarized at the tribal to family levels in Table 3.

COLLETIDAE

This family is considered the most primitive among bees, partly because of the short mouthparts which resemble those of wasps. The family is probably paraphyletic, held together by resemblances which are primitive features. It is difficult to find any derived character common to colletids and not also found in other groups of bees. A candidate for such a character, however, is the secretion by adult females of a cellophanelike membrane to line the cells. Other bees either do not line the cells, or line them with more waxlike materials.

Following Jander (1976) and Michener, Winston & Jander (1978), I assume that the colletid subfamilies Euryglossinae and Hylaeninae which carry pollen to the nest internally, in the crop, are ancestral in this respect to bees that carry pollen externally in a scopa. The pollen-gathering movements of the hylaeines and, presumably, the euryglossines are such that only pollen sticking to the forelegs and head can be swallowed for transport in the crop, while pollen that lodges on the other legs, the thorax, and the abdomen must be largely lost. This seems inefficient. It is unlikely that hairy bees that carry pollen in a scopa, and that can transfer to the scopa pollen sticking to both head and thorax, as well as all the legs, would evolve into forms inefficient in these respects like hylaeines.

Of these two subfamilies, the Euryglossinae are more primitive in various features than the Hylaeinae. The former are found only in Australia, being represented by 27 genera and subgenera, four of which reach Tasmania (Michener,

1965a and subsequent papers by E. Exley). None occurs in New Guinea and the subfamily is scarce in tropical northern Australia. Most species are restricted to or collect pollen primarily from flowers of Myrtaceae (Michener, 1965a). It is therefore possible that the relative scarcity of Myrtaceae in other continents is responsible for absence of Euryglossinae in those continents. There are, however, many Myrtaceae in South America. This plant family appears in the Upper Cretaceous fossil record and presumably migrated across Antarctica, but the euryglossines may not have tolerated such a cool temperate, probably forested route. The climatic tolerance of Euryglossinae appears to be limited, as suggested by the scarcity of the group in cool, moist Tasmania as well as in the tropical north of Australia.

The subfamily Hylaeinae is widespread but is diverse and a major faunal element only in Australia (Michener, 1965a; Houston, 1975), where there are 28 genera and subgenera, *Hylaeus* with 14 subgenera being the largest genus. Of these subgenera three reach Tasmania, one reaches New Zealand, and one has a species in the Tuamotu Islands. Obviously, Hylaeinae are capable of occasional long distance, over-water dispersal. New Zealand species of *Hylaeus* are similar to certain Australian ones and must have arrived relatively recently over water. The distance is 1,600 km, with no significant intervening islands. Although many Australian Hylaeinae occur in temperate areas, the group is most diverse in subtropical and tropical Australia, where most of the forms that are segregated from *Hylaeus* as distinct genera occur. The genus *Palaeorhiza*, while found in subtropical and tropical Australia, is most abundant and diversified in New Guinea, from which it ranges as far west as Timor and Flores and as far east as the Solomon Islands and the New Hebrides. *Gephyrohylaeus* is a small group which ranges from northern Australia to Borneo. No other genus of bees has a similar range.

In Africa there are two distinct hylaeine genera (both unnamed), one in the high equatorial mountains, the other in the Cape region (R. Snelling, in litt.). They have no obvious relations to particular Australian genera, but might be part of the same complex.

The genus *Hylaeus* is worldwide, less diverse in other continents than in Australia, but with a specialized derivative called *Nothylaeus* in Africa and Madagascar. Cladistic relationships among hylaeine genera have not been investigated, but my belief is that *Hylaeus* (or certain groups thereof) is primitive and that most or all of the other genera are derived from it.

There are about 11 palearctic subgenera of *Hylaeus* (Popov, 1939). Thus there is a secondary center of diversity within the genus in that region. One Palearctic subgenus, *Nesoprosopis*, is represented by only one species in Europe but about half of the Japanese species belong to it (Hirashima, 1977); it is found also in the Bonin Islands and in Hawaii. In the latter, extensive speciation (about 60 species) has occurred (Perkins & Forel, 1899).

Three of the Palearctic subgenera are also abundant in the Nearctic region, where two small strictly Nearctic subgenera also occur (Snelling, 1966). Of about five Neotropical subgenera, two reach the southern Nearctic region. The genus is present in the Antilles (Alayo Dolmau, 1973). The African subgenera have not been elucidated in print but there are six of them (Snelling, in litt.), at

least two of which reach Madagascar. Relationships among the subgenera of *Hylaeus* have not been investigated on a world basis, but there is no obvious similarity among the subgenera found in Australia, South America, or Africa. The species of the Oriental region have mostly not been assigned to subgenera (except for *Hoploprosopis* in the Phililppines), but they are not numerous and show no suggestion of relationships to Australian forms. Presumably they are of Asiatic origin. The Neotropical and described African forms (including the genus *Nothylaeus*) also seem to be related to northern subgenera (Snelling, in litt.). *Hylaeus* in South America is best represented in tropical and subtropical regions and is absent in the Araucanian region, facts which also argue against an interchange with Australia either directly or through Antarctica.

Australian forms of *Hylaeus* include some with at least certain characters (e.g., pygidial plate) more primitive than in any other Hylaeinae (Michener, 1965a). In view of this and the presence of Euryglossinae in Australia, it is reasonable to suppose that Hylaeinae arose on the southern continents, presumably in Australia. It is not clear how they reached other continents, except that it was not via New Guinea and the Indonesian area to Asia during the last 15 m.y. that the route has been more or less open, for this is too recent and also would require them to traverse a large land area, the Oriental region, where the subfamily is not well represented. The secondary center of diversity in the genus *Hylaeus* in the Palearctic region may have been populated from Africa, or via India across a reduced Indian Ocean, or both, in the early Tertiary and may well have served as the source for the New World, as well as perhaps the present African and the southeast Asian forms of this genus. The best route between southern and northern continents was via northern Africa to Eurasia.

The subfamily and perhaps even the genus *Hylaeus* might have appeared in the Upper Cretaceous (say 70 m.y. BP) and been dispersed by continental movement. Lack of similarity between the Australian and South American faunas, however, argues against this hypothesis, for those continents were connected through cool temperate Antarctica until about 38 m.y. BP. *Hylaeus* lives in such climates at the present time—for example 15 species of various subgenera are known from Finland (Elfving, 1968).

The subfamily most closely related to the Euryglossinae and Hylaeinae is the Xeromelissinae (= Chilicolinae), best developed in the Araucanian region but extending more sparsely into Brazil and north to St. Vincent in the Lesser Antilles and to the southern part of the Mexican Plateau. It seems to be absent from wet lowland tropics but can be found in either dry lowlands such as northeastern Brazil or at middle altitudes such as in the Colombian Andes or the central plateau of Costa Rica. Presumably the ancestors of Xeromelissinae became isolated from those of Euryglossinae and Hylaeinae at least 38 m.y. BP when opportunities for more or less direct migration between Australia and South America via temperate Antarctica no longer existed.

The subfamily Colletinae is divided into two tribes, the ancestral Paracolletini and the widespread Colletini. The Paracolletini, presumably the most primitive (Michener, 1944) of the hairy bees that carry pollen externally on the scopal hairs (in this case on the hind legs and sometimes also on the abdominal sternum),

have a disjunct, largely panaustral distribution. There are 27 genera and subgenera in Australia (Michener, 1965a), two of which reach Tasmania. One Australian subgenus also reaches New Zealand, where it occurs with a closely related subgenus restricted to New Zealand. A different Australian subgenus has one species in New Caledonia. None of the forms occurring in New Zealand or New Caledonia appears to be relictual; rather they must be relatively recent over-water migrants from Australia, to judge by their similarity to Australian forms. To the north one subgenus reaches New Guinea and Misool. The great abundance of species and higher groups, however, is in the temperate parts of Australia, with but few species, all in the genus *Leioproctus*, in outlying regions. The presence of a few species of the genus in New Zealand and one in New Caledonia indicates an ability to cross rather large water gaps. Since *Leioproctus* nests in the ground, such migration must be by bees being blown or possibly clinging to detritus. The only paracolletine known to nest in wood, *Callomelitta*, is restricted to temperate Australia.

The closest relatives of Australian Paracolletini are members of the tribe found in South America. About 17 genera and subgenera are found there. (More have been described; I have estimated that there are 17 more or less equivalent in distinctness to those in Australia.) As in Australia, the genus *Leioproctus* is the predominant group (Michener, 1965a), but none of the subgenera is the same in the two continents. The species are common in the Araucanian Region but also abundant and morphologically diverse in the southern part of eastern South America (southern Brazil to Argentina). In smaller numbers they range north to the arid parts of northeastern Brazil, as well as through the Andes. A single genus, *Eulonchopria*, occurs not only from central Brazil to Argentina but also in arid parts of Mexico and southern Arizona (Sonoran region). This is the only penetration of the Northern Hemisphere by Paracolletini, and the genus is the only amphitropical paracolletine (Michener, 1963). Presumably the separation of South American and Australian Paracolletini dates to at least 38 m.y. BP when more or less direct migration through Antarctica between these two continents became impossible.

The only remaining Paracolletini, the two closely related genera of southern Africa, have some characters in common with the Euryglossinae that indicate either a common ancestor or convergence. The African genera (*Scrapter*, *Parapolyglossa*) may have been isolated from those of Australia and South America since Africa, Antarctica, and Australia drifted apart. An interrupted pathway for migration through Madagascar and India from Africa to Australia existed in the Upper Cretaceous, but relatively long distance over-water transport may have been involved in the dispersal of Paracolletini to Africa. Only one successful introduction is necessary to explain all the African Paracolletini. They occur both in the arid Cape region and in mesic eastern South Africa, but are morphologically a compact group. (A parallel is the Restionaceae, likewise homogeneous in Africa; Raven & Axelrod, 1974.)

The tribe Colletini, the sister group of or perhaps a derivative of the Paracolletini, is found on all continents except Australia (also absent from Madagas-

car). There is only one major genus, *Colletes*; it has numerous species in all continents except Australia. *Colletes* probably originated in the south, however. Its only close relative is an unnamed genus of the Araucanian region which contains several species obviously affiliated with *Colletes*, but lacking some of its special features and therefore more like Paracolletini. If *Colletes* arose in South America, as seems likely considering both its Araucanian relative and the distribution of the Paracolletini, it must have spread to other continents via North America or possibly across the narrow Altantic to Africa and Europe. While land connections between the Americas date only to 5.7 m.y. BP, island hopping would have been increasingly possible from the Oligocene onward, and is very probable considering the abundance and diversity of *Colletes* species in the Holarctic region and the presence of *Colletes* today in the Greater Antilles. Failure of the genus to reach Australia recently by island hopping can be attributed to its absence from southeast Asian lowlands, Indonesia, and even the lowlands of India. It occurs in the lowland moist tropics in the Americas, but not in Asia and probably not in Africa.

The subfamily Diphaglossinae consists of large, robust, fast-flying colletids restricted to the Western Hemisphere (Michener, 1966). The three genera of the tribe Diphaglossini are restricted to the Araucanian region. The two genera of Mydrosomini are tropical forest bees from Brazil to southern Mexico. The monotypic tribe Ptiloglossidiini is from northern Argentina. The tribe Caupolicanini contains seven genera and subgenera. Of these, *Ptiloglossa* is largely tropical, ranging through the moist tropics although extending beyond the tropics both in Argentina and in North America (to Southern Arizona). *Crawfordapis* is restricted to Mesoamerican mountains. The genus with the most interesting distributional pattern is *Caupolicana*. The subgenus *Caupolicana* s. str. occurs in the Araucanian and adjacent parts of South America, with a few species extending well north in Peru, and reappears in the North American deserts, extending to Arizona and beyond, into the plains, to western Kansas. There is also a single species in the southeastern United States. The subgenus *Zikanapis* also has a disjunct amphitropical distribution—southern Brazil and adjacent warm south temperate regions, north in the Andes to Colombia, and the Mexican plateau, north to southern Arizona. The subgenus *Alayoapis* is known only from Cuba and Hispaniola. Seemingly the Diphaglossinae arose in South America, probably from a paracolletine stock, and invaded the Antilles and southern North America during the Tertiary, perhaps by crossing water or in some cases wet tropical areas, as did certain plant families like the Loasaceae and Zygophyllaceae (Raven & Axelrod, 1974: 628).

The only remaining colletid group, perhaps not properly placed in this family, is the subfamily Stenotritinae, consisting of two genera restricted to the temperate parts of Australia (Michener, 1965a).

In summary for the Colletidae, the family is clearly primarily southern, i.e., of Gondwanaland origin, only the genera *Colletes* and *Hylaeus* becoming widespread (the former absent in the Orient and Australia) and now occupying the Laurasian as well as the Gondwanaland continents.

OXAEIDAE

This is a small family limited to the Western Hemisphere. It contains four genera and subgenera (Hurd & Linsley, 1976) of which *Oxaea* is tropical (Brazil to southern Mexico), *Notoxaea* is southern (South Brazil to northern Argentina), and *Protoxaea* and *Mesoxaea* occur in the North American deserts and on into eastern Texas and Louisiana. The last three taxa are commonly united in a single genus *Protoxaea*, which in this sense is amphitropical. In view of its limited distribution in the Nearctic region, the family is presumably of Neotropical origin.

HALICTIDAE

This family contains three subfamilies, of which one, the Dufoureinae (Michener, 1965b), consists mostly of morphologically specialized forms restricted to particular flowers and often uncommon, but retains a number of ancestral features such as cocoon-spinning by larvae. It is presumably the sister group to all the other Halictidae. It is principally Holarctic, with about eight Palearctic and six Nearctic genera and subgenera, two of them (*Dufourea* and *Halictoides*) in common. The area with the largest number of species and with great morphological diversity is the western United States. From California 74 species are recorded (Moldenke & Neff, 1974); comparable Palearctic areas have only 4 to 8. Of two Palearctic genera, *Systropha* and *Rhophites*, each has a species or two reaching southern Africa, where there is a distinctive subgenus of *Systropha*. *Systropha* also occurs in tropical areas, e.g., West Africa, India, Sri Lanka, and southeast Asia, although it is most abundant in xeric areas of the Mediterranean basin and thence eastward toward central Asia.

In the Western Hemisphere, the northern genera occur south only into the Mexican plateau. There is, however, a geographically isolated genus, *Penapis*, containing two species in Chile. It is possibly most closely related to genera such as *Sphecodosoma* of Texas and the southwestern United States, but is very different, and the two have presumably been diverging for a long time. As no American members of the subfamily are known from the tropics, *Penapis* presumably reached Chile across a substantial uninhabited gap.

The enormous subfamily Halictinae is divided into three tribes. The tribe Augochlorini, containing 31 genera and subgenera (Eickwort, 1969), is primarily Neotropical, with three otherwise Neotropical genera, *Augochlora*, *Augochlorella*, and *Augochloropsis*, extending north in eastern America as far as southern Canada, and two others, *Pseudaugochloropsis* and *Temnosoma*, barely reaching the southwestern United States. Eight genera range from North America to Argentina, and ten are restricted to the area of southern Brazil to Argentina, which thus seems to be the region of maximum diversity for the tribe. This tribe is poorly represented in the North American deserts and only a single species is found in the Pacific coast states. In the Araucanian area, however, it is represented by the genus *Corynura* with two subgenera and rather numerous species. This genus has some characters (e.g., a galeal comb) unusual in halictines and presumably primitive, but it is unrelated to Australian halictines which are all in different tribes. It is likely that aridity and physiographic barriers have made the Arau-

canian area a refuge for this primitive type, which has perhaps disappeared elsewhere in South America, except for the minute species of the related genus *Halictillus* in southern Brazil and Argentina. Augochlorini are well represented in tropical forested areas and four genera have reached the Antilles.

The tribe Nomioidini, containing a single genus *Nomioides*, is found in the steppe, savanna and desertic areas of the Old World from the Canary Islands, the Mediterranean area, and even central Europe, throughout Africa, eastward to Madagascar and across Asia to Taiwan, the Philippines, the Sunda Islands and with a single species reaching middle latitudes in Australia (Michener, 1978a). It is absent from forested areas, including (so far as known) New Guinea and nearby islands. It has obviously crossed rather broad water or forest areas to reach parts of its range.

The tribe Halictini (Michener, 1978a) is represented by many species on all continents. There are seven strictly American genera. One group consists of *Habralictus* and *Caenohalictus* which range from northern Argentina to tropical parts of Mexico (Michener, 1979), the latter genus also occurring in the Araucanian region. The second group consists of the south temperate *Pseudagapostemon*, the Araucanian *Ruizantheda*, the tropical forest genus *Rhinetula*, the Mesoamerican montane *Paragapostemon*, and the widespread (Canada to Argentina) *Agapostemon*. The last is well represented in the Antilles (Roberts, 1972), but absent from the Araucanian region.

Africa has a distinctive group of Halictini (Michener, 1978a), none of which is closely related to those of South America or Australia. *Zonalictus* ranges throughout sub-Saharan Africa and into the Arabian peninsula; *Patellapis* (3 subgenera) is restricted to southern Africa, both arid and savanna regions. *Pachyhalictus* contains only one African species, from Malawi to Natal, but there are numerous Oriental species (India to the Philippines and New Guinea) and even one in northern Australia. *Thrinchostoma*, with three subgenera, occurs throughout Africa except the Cape region, is particularly well represented in Madagascar (where a derived parasitic genus *Parathrincostoma* occurs), and ranges in Asia from southern India to Viet Nam, Kalimantan, and Java. A final member of the African group of genera is *Thrincohalictus*, not found in Africa but represented by a single species in Asia Minor.

The remaining members of the tribe Halictini are mostly in large, widely ranging genera, 20 or more genera and subgenera being involved. *Lasioglossum* and its subgenera occur on all continents, although relatively poorly represented in the Neotropics where their place is partly taken by the Augochlorini. The six Australian subgenera are all restricted to that region, except that one of them, *Ctenonomia*, ranges to southeast Asia. Another, *Parasphecodes*, extends to New Guinea and a third, *Austrevylaeus*, to New Zealand (Michener, 1965a). Clearly the New Zealand forms are relatively recent over-water arrivals from Australia. Africa also contains a rich fauna with several distinctive groups of *Lasioglossum* (e.g., *Oxyhalictus*), none of them closely related to congeners in Australia or South America. The Holarctic region contains several widespread subgenera with many species—*Lasioglossum* s. str., *Evylaeus*, *Dialictus*, as well as a few more restricted subgenera such as *Sphecodogastra*, which is oligolectic on flowers

of Onagraceae in the western United States, and the parasitic (on *Dialictus*) genus or subgenus *Paralictus* primarily in the central and eastern United States. Neotropical forms, which range all the way to Argentina and Chile, are mostly *Dialictus* with some *Evylaeus*, both groups consisting of species rather close to members of the same subgenera in the Nearctic region and not similar to Australian or African subgenera of *Lasioglossum*. Thus the South American forms must have arrived from the north at some relatively recent time. This could well have been before continental connections developed 5.7 m.y. ago, for these bees are evidently good island hoppers. *Dialictus* occurs on the Antilles, and on such small and isolated oceanic islands as Bermuda and Fernando de Noronha.

Halictus with its three subgenera is primarily Palearctic with many species and much diversity in Eurasia. One subgenus, *Seladonia*, extends south throughout Africa, India, and Southeast Asia and also contains a few Nearctic and Mesoamerican species and one that occurs in central Brazil. Another large Palearctic subgenus, *Halictus* proper, contains four Nearctic species representing two Palearctic groups and thus at least two migrations from Eurasia to North America. One of the North American species reaches Colombia and Trinidad and occurs also in Cuba. The third subgenus, the palearctic *Vestitohalictus*, is largely restricted to the Mediterranean and Asiatic xeric regions.

Homalictus is a large Australian genus, also particularly richly developed and diverse in New Guinea, with a smaller number of species ranging northwest as far as the Philippines and India. The genus has crossed the water gaps rather readily, for some species are similar throughout this wide area, and some species exist on oceanic islands eastward as far as Micronesia and Samoa. Most of the insular species occur on several islands or island groups (Krombein, 1950). The distinctive genus *Echthralictus* has arisen as a parasite of the local *Homalictus* in Samoa.

Finally, there is the genus *Sphecodes* and its relatives (Michener, 1978b), found on all continents but barely penetrating (2 species) northern Australia from Indonesia or New Guinea. Other continents contain many species. Probably the most primitive species, and those most closely related to similar genera (the Neotropical *Microsphecodes* and *Ptilocleptis*), are South American. There are Chilean species and they are not at all similar to Australian ones but are related to those in other parts of South America. The subgenera of the Holarctic region have not been worked out, but there are obvious similarities between the faunas of the northern continents and also Africa. In Africa there is also a related genus, *Eupetersia*, a specialized derivative of *Sphecodes*, found also on Madagascar, with a species on the Seychelles and another in southern India (Michener, 1978b).

The third subfamily of Halictidae, probably the sister group to the subfamily Halictinae, is the Nomiinae. Its classification has not been well studied. It is primarily a tropical and subtropical group of the Old World, and most of the species are tentatively placed in *Nomia*. The greatest diversity is found in Africa (including Madagascar), but there are a few species in the Mediterannean basin and southern Europe, north to Hungary and southern Germany. Eastward, the group is well represented across southern Asia to China, Japan, the Philippines, New Guinea, the Solomon Islands, and Australia. In Asia most of the groups appear to

be the same as those found in Africa, although *Hoplonomia* is primarily Asiatic but reaching through Indonesia to New Guinea and Australia and westward only to Madagascar, not to Africa. In New Guinea there are three groups not found elsewhere (*Reepenia*, *Ptilonomia*, and *Mellitidia*) or reaching only nearby islands and northern Australia (Michener, 1965a). The principal Australian group, *Austronomia*, also ranges across Indonesia to the Philippines, Taiwan and southern Asia. Its ability to colonize islands is shown by the presence of a species, similar to some of those of Australia, on New Caledonia.

Two nomiine groups (*Epinomia-Dieunomia* and *Curvinomia-Acunomia*) have reached North America, no doubt across the north Pacific at a time of more mild climate than the present. They have diversified to a limited extent, each having several western species and one spccies reaching or limited to the southeastern states; each has been divided into two subgenera as indicated in parentheses above. Each ranges south well into Mexico, and *Acunomia* has one species in Cuba and the Bahamas (Ribble, 1965). The Nomiinae are otherwise absent in the Neotropical region.

In view of the largely northern distribution of the subfamily Dufoureinae and the rich representation of the other subfamilies in the Holarctic region, it seems likely that the origin or at least the initial radiation of the Halictidae was in the Laurasian continents. There were early major invasions of the southern continents, however, followed by extensive radiations, especially of Nomiinae in Africa, of Augochlorini in South America, and of Halictini in all three southern continents.

ANDRENIDAE

There are two subfamilies of Andrenidae with very different distributional patterns. The subfamily Andreninae includes the huge genus *Andrena* with probably over 1,000 species distributed throughout the Holarctic area. In North America there are some 35 subgenera. Several subgenera and even a few species are holarctic, indicating multiple dispersals between the two northern continents. There are a number of species in the highlands of east Africa; and a few extend southward, one to the Cape of Good Hope. Even west Africa is not without *Andrena*—there is one on the island of São Tomé in the Gulf of Guinea. In India the genus reaches the lowlands, for example in Punjab, and in southeast Asia it is present in mountains. It is not known from Indonesia, the Philippines, etc. In America, while well represented in the Mediterranean climatic area of California, the genus is scarce in the Sonoran area but extends south in small numbers through Central America, the southernmost record being in savanna areas near sea level not far from the Panama Canal Zone.

Aside from *Andrena*, the subfamily includes *Ancylandrena* and perhaps *Megandrena* (with two subgenera) from the Sonoran desert and semidesert (Zavortink, 1974) and the highly disjunct small genera *Orphana* and *Euherbstia* from Chile (Rozen, 1971).

The Panurginae is a diversified group with many genera. The subfamily is most abundant and diverse in the Western Hemisphere, there being about 38

genera and subgenera in the Nearctic region (including the genus *Perdita* with some 500 species in 20 subgenera) and over 20 genera and subgenera (some undescribed) in the Neotropics. The subfamily is present but poorly represented in the lowland and even montane tropics (Michener, 1954; Friese, 1916, 1921), but there is evidence of north-to-south or south-to-north dispersal of various groups at different times. The panurgines with most ancestral characters occur in both North and South America. Examples are *Psaenythia* in South America and its relative *Protandrena* in North America, and *Cephalurgus* and *Pterosarus* (not similar to one another) in South and North America respectively. Drs. J. G. Rozen and H. Toro (in litt.) suggest that from such basic groups *Heterosarus* arose; it or close relatives range from Canada to Argentina, although they are scarce in the tropics. A derived group of related genera found in both continents contains *Nomadopsis*, *Hypomacrotera* and *Calliopsis* in North America and *Acamptopoeum* and probably *Liopeum* in South America. *Calliopsis* includes a species ranging as far south as Panama and *Acamptopoeum* includes a species that ranges as far north as Colombia.

Since some of the relatives in the two continents are quite different from one another, it seems certain that some of the dispersal occurred well before there were continental connections (5.7 m.y. BP). Most panurgines occur in rather xeric or at least not forested situations. In North America, most species and genera are western and especially southwestern. Presumably there was migration by island hopping between the American continents, but if so, conditions were perhaps rather different from those of the present, for panurgines are not known from the Antilles and are not common in Central America (only two Panamanian species, Michener, 1954) or northern South America.

Outside of the Americas the Panurginae is a small group consisting of about nine genera and subgenera in the Palearctic region (one of them, *Panurginus*, found also in the Nearctic) and four genera in eastern and southern Africa. *Melitturga*, one of the genera found in Africa, is also widely distributed in the Palearctic and two others, *Meliturgula* and *Poecilomelitta*, range into the Arabian peninsula (Baker, 1972), the latter also to Iran (Popov, 1967b). *Meliturgula* also occurs in Madagascar.

The family Andrenidae is absent in Australia, the Indonesian region, and most of southeast Asia.

Probably the family Andrenidae arose or initially radiated in the Laurasian continents, the main area of occurrence of the Andreninae. When genera rather than species are considered (3 genera in North America, 2 in South America, only one in the Old World), the Western Hemisphere seems to take on special importance for the Andreninae, as for the Panurginae. However, except for *Andrena*, all the genera are small, perhaps relictual, and many show little about their areas of origin. The Panurginae, like the Augochlorini in the Halictidae, probably reached South America early in the Tertiary, and there radiated, various lines eventually returning to and reradiating in the Nearctic region, some genera probably then going back to South America, and a few genera spreading from North America to the Old World.

MELITTIDAE

This is a small family, although divided into four subfamilies. Of all the families of short-tongued bees (i.e., this and previously discussed families), this is the only one sharing certain characters with the long-tongued families, e.g., the form of the mentum and submentum. It is therefore assumed to be an archaic group, either the sister group to all the long-tongued bees or a paraphyletic group from which the long-tongued bees arose.

The Macropodinae contain a single small Holarctic genus with a Chinese species placed in a separate subgenus. The subfamily Ctenoplectrinae contains a single Paleotropical genus which is widespread in Africa, where there is also a parasitic subgenus, but is absent in the southwestern Cape region as well as in Madagascar; it occurs also in southeast Asia, the Philippines, Indonesia, New Guinea, and northern Australia. The genus ranges well north into the temperate parts of China and even into the maritime USSR (Popov, 1956); otherwise it does not occur in the Palearctic region.

The remaining subfamilies, the Melittinae and Dasypodinae, are both more common in Africa, especially southern Africa, than elsewhere in the world. Each is represented there by a small number of genera and subgenera. Each is absent from the moist tropics, although *Meganomia* in the Melittinae occurs in equatorial savannas of east Africa as well as in southern Africa. The Melittinae range also through much of the Holarctic region, being represented by several subgenera of *Melitta*. They are less abundant in North America than in Eurasia. The Dasypodinae are represented in the Palearctic region by one widespread genus, *Dasypoda* (Europe to Japan, especially abundant in semiarid areas like the Mediterranean basin). The most interesting distributional pattern in the family is that of the dasypodine genera (or subgenera) related to *Hesperapis*. *Hesperapis* is in the western United States and northern Mexico, with one or two species ranging into the plains and as far north as North Dakota; *Capicola* and its close relatives, in South Africa (mostly Cape Province); and *Eremaphanta*, in arid parts of central Asia (Popov, 1957) such as Turkestan. Regardless of the rank (generic or subgeneric) of these bees, they consistute a group with a highly disjunct distribution, being found in three widely separated arid areas of the world. The family is absent from Australia (except one *Ctenoplectra* in the far north), South America and Madagascar; except for *Ctenoplectra* the family is also absent from southern Asia and nearby islands.

I believe that the Melittinae and Dasypodinae are clearly related and quite likely of African origin, from which continent they reached Eurasia, and thence North America in small numbers. The Macropodinae, entirely Holarctic, and the Ctenoplectrinae, centered in Africa and extending thence to the Oriental and Australian areas, may or may not be closely related to the first two subfamilies.

FIDELIIDAE

This small family appears to be the sister group to the Megachilidae. It contains only three small genera, two (*Fidelia* and *Parafidelia*) living in arid western parts of southern Africa, the other (*Neofidelia*) living in arid central Chile. The

last direct migration route between Africa and South America was closed about 90 m.y. BP, in the lower Upper Cretaceous, and in any case, was through the tropics. The family must have had a wider distribution in Upper Cretaceous and Paleogene time, and dispersed across oceans which were, however, narrower than at present. There are very few links between the floras of temperate South America and Africa (R. Raven, in litt.) and no possibility for direct migration between these areas seems to have existed during the entire history of the group. (Nests are in dry soil; there is no possibility of nests being transported across water.)

[Since this paper was written, Rozen (1977a) has reduced the fideliids to subfamilial rank in the Megachilidae. Because their rank is of little importance for the present account, and because their proboscis lacks distinctive megachilid characters and is more like that of anthophorids, I have not altered the manuscript. The relationship of fideliids to the base of the megachilid stem is clear, however.]

MEGACHILIDAE

The Megachilidae (together with the Fideliidae) are the bees in which females of nonparasitic species transport pollen on the ventral abdominal brush or scopa and not on the hind legs. The family is divisible into two subfamilies, the Lithurginae and the Megachilinae. The former retains a number of ancestral characters also found in other families of bees, but it also possesses derived features of its own showing that it is a holophyletic sister group of the Megachilinae. The Lithurginae are most diverse in temperate South America where they are represented by the largely Araucanian genera *Lithurgomma* and *Trichothurgus* (Moure, 1949). All continents are inhabited by a few species of the remaining genus, *Lithurge,* which occurs in dry to moist tropical to temperate areas. One subgenus is restricted to the Western Hemisphere, where it is absent in forested tropical regions and is therefore amphitropical. It is present in the Antilles. The other subgenus is found in Europe, Asia, Africa, and Australia and intervening islands, also in New Caledonia and all the island groups eastward to Tahiti (Michener, 1965a) and Micronesia (Krombein, 1950). It also contains a species in northeastern Brazil. Obviously the species of *Lithurge*, which nest in old wood, have been good at crossing water. However, there are few if any insular endemics. Some of the dispersal may have been by primitive man.

The subfamily Megachilinae contains the tribes Megachilini and Anthidiini, both widespread and with numerous genera and subgenera, and the tribe or divergent anthidiine group Dioxini, of more limited range. Few Megachilinae exhibit disjunct or otherwise unusual distributions.

We consider first the relatives of *Megachile*, i.e., those Megachilini without arolia. Of 16 subgenera of *Megachile* in the Nearctic region, three occur also in the Palearctic and eight occur also in the Neotropics. Of these eight, six are primarily Neotropical and have only one Nearctic species or reach only the southernmost United States, and two are primarily Nearctic with a few Neotropical species. In all there are 17 Neotropical subgenera, most of them restricted to that area (Mitchell, 1943). Of seven African subgenera (Pasteels, 1965), one (*Eu-*

tricharaea) is wide-ranging in the Palearctic, Oriental, and Australian regions, the others probably restricted to Africa (although the southern Asian and Madagascar species have not been classified subgenerically and may include some members of African subgenera). As to Australian subgenera, in addition to *Eutricharaea*, one is restricted to Australia and another ranges from northern Australia to southeast Asia and India (Michener, 1965a).

The genus *Creightonella* is most common and diverse (2 subgenera) in Africa but also extends across southern Asia from India to southern China and southeast Asia, and on as far as New Guinea and the Solomon Islands.

Chalicodoma, consisting of *Megachile*-like bees not equipped to cut leaves, is primarily Paleotropical but there are several Mediterranean species and one that reaches central Europe. There are 13 African subgenera (Pasteels, 1965), two or three of which are also Palearctic, two of which range to southern Asia, and one of which, *Callomegachile*, occurs not only in Africa but all the way from India to Japan, Taiwan, the Philippines, New Caledonia, and the northern half of Australia. There are eight subgenera in Australia (Michener, 1965a), two of which range across Indonesia to southeast Asia, one (*Callomegachile*) far beyond as indicated above. A ninth subgenus in the Australian region ranges from New Guinea to Japan.

The groups listed above, related to *Megachile*, have distributions that suggest dispersal could have occurred during a period when the continents occupied more or less their present positions. Each taxon that occurs on more than one continent or in more than one zoogeographic area occupies neighboring continents or areas. The only exception is noteworthy and not easy to explain. The only American group of *Chalicodoma* is *Chelostomoides*, a widespread Nearctic subgenus especially well developed in the Madrean region, and with a few species in Central America and northern South America. It is absent in southern South America. Strangely, it is almost identical to the large subgenus *Hackeriapis* of Australia (two species in New Guinea savanna areas). There seems to be no evidence for or against any of the likely explanations for this disjunction. Since all the other subgenera of *Chalicodoma* occur in the Eastern Hemisphere, it seems very probable that *Chelostomoides* came in some way from that hemisphere.

Megachile-like bees have been excellent island-hoppers. There are numerous species of several groups on the Antilles; numerous species range widely through Indonesia; *Megachile* species (subgenus *Eutricharaea*, which is also African, Palearctic, Oriental, and Australian in distribution) extend to New Caledonia and eastward on all island groups to Tahiti, Micronesia, and Hawaii. There is little island endemism, suggesting recent dispersal, but some of the Pacific species do not appear to occur on any continent. None occurs in New Zealand.

The only remaining genus of Megachilini without arolia is *Coelioxys*, most species of which are parasites in the nests of the megachiline genera listed above. Worldwide studies of its groups are even less complete than for *Megachile*. *Coelioxys* is especially abundant in South America, and 14 subgenera have been named for the species of the Western Hemisphere (Mitchell, 1973). Two such subgenera are Holarctic while four are mostly Neotropical but extend into the

Nearctic region. The remainder are either strictly Nearctic (3) or strictly Neotropical (5). Two of the Neotropical subgenera have species on the Antilles.

In the Old World there is perhaps greater morphological diversity among subgenera than in the New World, but there are fewer recognized subgenera (only 3 in Africa, Pasteels, 1968). One, *Hemicoelioxys*, is monotypic and known only from tropical Africa. Another, the very distinctive *Liothyrapis*, occurs in Africa, the Mediterranean basin, and eastward across southern Asia to the Philippines, New Guinea, and Australia. The third is perhaps a catch-all. Unlike *Megachile* and *Chalicodoma*, *Coelioxys* is poorly represented in Australia and does not extend to Pacific Islands beyond the Solomon Islands and the Philippines.

The remaining Megachilini, those with arolia, have a generally different distributional pattern, being primarily Holarctic and for some groups also African. *Osmia* is Holarctic, four of its subgenera (*Osmia* s. str., *Melanosmia*, *Chalcosmia*, *Diceratosmia*) occurring in both northern continents. Several other subgenera are restricted either to North America or to Eurasia. *Hoplitis* (including *Anthocopa*) is also largely Holarctic, and two of the subgenera, *Alcidamea* and *Formicapis* (the latter perhaps a distinct boreoalpine genus of one species), are Holarctic. *Hoplitis* extends southward to southern India and through east Africa to Cape Province. *Hoplitis* also appears to be ancestral to a variety of taxa in the xeric warm temperate regions such as California, the Sonoran region, the Mediterranean basin, Turkestan, etc. In the southwestern United States there are about 13 such xeric-adapted genera and subgenera, several of them falling under the genera *Ashmeadiella* and *Proteriades*. The Old World xeric segregates of *Hoplitis* superficially resemble some of those of the New World but appear to be independently derived. Some such as *Protosmia* may not be segregates, but may be sister groups to *Hoplitis*; the Pacific Coast (North America) *Chelostomopsis* may be an American *Protosmia* (Popov, 1961). Like *Osmia*, *Hoplitis* does not occur in southeast Asia, Australia, or the Neotropical region.

Heriades is a widespread genus. It occurs throughout the Holarctic area and is unusually abundant and diversified in Africa, where a few related genera or subgenera occur. *Heriades* is present in Madagascar. Some of the African species seem closely related to European species. It may be that neither of the two American subgenera occurs in the Old World. In the Western Hemisphere *Heriades* extends southward to the Antilles (Alayo Dolmau, 1973) and Panama. In the Eastern Hemisphere, it ranges widely in the Oriental region and eastward to the Philippines and Micronesia (Krombein, 1950), but while it occurs in Borneo and Java, it is not known from the Lesser Sunda Islands, or other areas to the south and east.

Chelostoma is a Holarctic genus with a disjunct distribution in the middle latitudes, in America not or scarely entering Canada and only marginally entering the Sonoran area. In this continent it is restricted to the west but in the east is replaced by the closely related derivative called *Prochelostoma*.

The tribe Anthidiini has been divided into no less than 80 genera and subgenera in the Old World (Pasteels, 1968) and about 37 in the New World (Michener, 1948). The splitting has been more intense in the Old World, but nonetheless the tribe appears actually more diverse there than in the New World. The

majority of groups (26) are Mediterranean and Near Eastern, often extending to Central Asia, sometimes to east or even southern Africa. Only two groups are tropical west African, but several are found in east Africa and about 20 are largely or wholly restricted to southern Africa. Only a few African groups jump to India and southeast Asia, a distributional pattern common in the Megachilini. There are a few groups in tropical Asia (Pasteels, 1972), only one of which (*Pycnanthidium*) extends across Indonesia to the Solomon Islands and northern Australia. Otherwise Australia lacks Anthidiini. Madagascar has only one anthidiine; its relationships are with African forms.

Only three Palearctic genera reach the New World. One is *Anthidium*, a genus of arid to humid areas in the Holarctic and Neotropical regions as well as in India. The others are *Anthidiellum* and *Trachusa*, both of which are temperate climate genera (although the first ranges far into the American tropics); the American forms are sometimes placed in different subgenera than the Old World forms. In the Americas there are more groups in the moist tropics than in the climatically equivalent parts of the Old World. While there is some diversity in the Madrean area, and some genera are largely restricted to this region (*Heteranthidium, Heterostelis*), there is no such diversity as in the climatically equivalent Mediterranean and Asia Minor. The same is true of temperate South America. There are no striking disjunct distributions, except perhaps for *Bothranthidium*, found from southern Brazil to Northern Argentina and in northeastern Mexico. It has recently been taken in savanna areas of Costa Rica, however, so it may not be amphitropical; perhaps it occurs in drier areas across the equatorial region.

The anthidiines most like Megachilini and other bees, and hence probably most similar to ancestral anthidiines, are *Trachusa* and its subgenera (Pasteels, 1972). This group is primarily Palearctic although two subgenera (one, the Holarctic *Trachusa*) occur in the Nearctic region. It therefore seems likely that the tribe is of Palearctic origin. Peters (1972), however, shows that the South African *Aspidosmia* is an anthidiine, and argues that it has important ancestral characters.

There are no anthidiines in the Antilles. This fact, their scarcity on Madagascar in spite of several east African groups, and the extention of only one group eastward beyond Borneo and other continental islands of Asia, suggest that Anthidiini are far less effective in traversing water barriers than are the Megachilini. Nonetheless, the moderately rich South American fauna cannot have developed since the elevation of the present continental connection (except for the South American species of *Anthidium*), and shows no relation to the African (or the almost nonexistent Australian) fauna. Hence the present South American fauna, especially that of temperate South America, must have originated from earlier Tertiary island-hopping immigrants from North America or from transatlantic immigrants from Africa.

The tribe Dioxini consists of seven genera, all parasitic on other megachilids (Popov, 1947). All are Palearctic (mostly Mediterranean and eastward into arid parts of Asia), one of them, *Dioxys*, also occurring in western North America.

In summary for the family Megachilidae, the archaic subfamily Lithurginae may have originated in South America, where it is now most diverse. Its sub-

sequent dispersal was very broad and details cannot even be guessed at. The Anthidiini experienced their main radiation in the Palearctic and African regions; the ancestral forms like *Trachusa* are mostly in the former area, and it is likely that the tribe originated there and spread to other continents. The Dioxini no doubt also originated in the Palearctic, whence they spread to western North America. The osmiine Megachilini are primarily Holarctic and must have originated there, probably, like Anthidiini, in the Palearctic. The other (anaroliate) Megachilini are diverse in all continents and their area of origin or even principal areas of radiation cannot be identified.

ANTHOPHORIDAE

This large family consists of three subfamilies, the Anthophorinae, Nomadinae, and Xylocopinae. The Anthophorinae are a major subfamily of long-tongued bees, common and with many genera on all continents except Australia, where they are represented by only two genera. Zoogeographically the most interesting anthophorines are the Exomalopsini with the related or synonymous Ancylini. The former tribe is American, the latter Palearctic; the relationships need to be investigated but the Ancylini appear at present to differ from the Exomalopsini chiefly in distribution.

Of the 26 American genera and subgenera of Exomalopsini (Michener & Moure, 1957), at least 11 are restricted to temperate southern South America, the rest are widespread in the Neotropics or occur farther north in South America. Some genera, especially *Paratetrapedia*, occur abundantly in the wet tropics. Five groups, all subgenera of *Exomalopsis*, reach the southern United States, two of them being primarily desertic or Madrean and not or scarcely occurring in the Neotropics. One of these five also occurs in the Antilles and southern Florida, another reaches the central United States. The Old World representatives of the group, *Ancyla* and *Tarsalia*, occur in the xeric Mediterranean to Central Asian belt, *Tarsalia* curiously with a species in southern India also.

Whereas there are many distinctive exomalopsine genera and subgenera endemic to the southern temperate zone in South America, the climatically equivalent northern region contains only two endemic subgenera. This suggests a longer history in South America than in North America. The occurrence of *Exomalopsis* in the Greater and Lesser Antilles shows the possibility of intercontinental island-hopping. The last direct connection between South America and Africa was in lower Upper Cretaceous (90 m.y. BP). At the beginning of the Paleocene (about 64 m.y. BP) Africa and South America were about 800 km apart, and if there were islands more or less midway, the breadth of the water to be crossed at one jump would have been less than the present distance from Yucatán to Jamaica. Therefore dispersal between Africa and South America could account for the present Old World distribution of the Exomalopsini-Ancylini. On the other hand, North American Exomalopsini, perhaps adapted to rather arid conditions, could have arrived from South America via islands at any time during the Tertiary, and thence reached the Mediterranean area across the still narrow and island-dotted Atlantic.

The related tribe Pararhophitini (Popov, 1949) ranges from the Mediterranean basin to central Asia. It contains only a single genus, *Pararhophites*.

The tribe Tetrapediini, related to the Exomalopsini, is Neotropical—Mexico to Argentina, mostly in wet tropics. It consists of a single genus with two subgenera.

The tribe Melitomini, also related to Exomalopsini, consists of about eight genera and subgenera (Michener, 1954), all American, ranging from Canada to Argentina and Chile. Most of these taxa are either Nearctic or temperate South American, but *Melitoma* ranges through the tropics (South Dakota to Argentina). *Ptilothrix* and *Dasiapis* (a subgenus of *Diadasia*) are amphitropical, occurring in temperate parts of both North and South America, but absent in much of the tropics. The genus *Diadasia* as a whole also approaches such a distribution since it has both North and South American temperate subgenera (in addition to *Dasiapis*); it is, however, represented in the tropics (at least Panama and Brazil) by one small, rare subgenus, *Diadasiana*.

The tribe Eucerinodini contains a single Araucanian species while the Canephorulini contains one species from the desertic parts of Argentina.

The Eucerini is a large tribe well represented on all continents except Australia. The tribe is best represented in the Americas, where 53 genera and subgenera are recognized (Moure & Michener, 1955; LaBerge, 1957). In the Old World there is quite clearly less diversity than in the New World, but no comparative studies at the genus and subgenus levels have been made. It is therefore only possible to give some impressions about Old World forms.

About 25 genera and subgenera are known from the Nearctic region, several of them only entering its southern fringes (LaBerge, 1957). About 33 genera and subgenera occur in the Neotropics, mostly in southern South America but a few restricted to or extending through the tropics. *Alloscirtetica* is the best example of a temperate South American genus; it is richly represented in the Araucanian area but occurs also in other temperate southern areas. Several genera (*Peponapis*, *Svastra*, *Melissodes*, *Florilegus*) are widespread both in North and South America, although *Florilegus* is more abundant and diversified in South America and *Melissodes* far more abundant and diversified in North America. *Martinapis* occurs in the Sonorian and Argentine deserts, not in intervening areas, and there is a tendency toward such an amphitropical distribution in *Gaesischia* which seems to be absent in the wet tropics although present for example, in savanna areas of Costa Rica and in arid northeastern Brazil. In both *Martinapis* and *Gaesischia* the northern and southern representatives are in different subgenera, suggesting long isolation.

The numerous groups that must have dispersed between the American continents and the considerable evolution that has occurred in each continent suggests that part of the interchange must have occurred well before the union of the continents, presumably by way of island stepping-stones. That this is likely is indicated by the presence of five groups, *Ptilomelissa* (a subgenus of *Melissoptila*), *Florilegus*, and three subgenera of *Melissodes*, on the Antilles. All are widespread groups and the species on the islands are similar to those found on the continents.

Two of the North American groups (*Tetralonia-Synhalonia* and *Xenoglossodes-*

Tetraloniella) seem to be holarctic, although sometimes different names for them are used in the two northern continents, and the systematic relationships have not been properly clarified. The Palearctic *Eucera* is close to *Tetralonia*. Both *Eucera* and *Tetralonia* occur in the cool northern temperate areas or in early spring in warm temperate, xeric areas, and it is not surprising that this group has passed between the two northern continents. There are two or three other Palearctic genera that show no obvious relationship to American genera.

Eucerini are scarce in the Oriental region although the genera *Melissina* and *Thygatina* are present in Sri Lanka and the Indian peninsula. The tribe is absent in Malaysia and Indonesia. In Africa there is the apparently distinctive genus *Eucera* (with an undescribed species in south India), plus various species currently left in *Tetralonia*, probably only for lack of adequate study. There are similar species in Madagascar. None of the African forms shows close relationships to species of other continents.

The Anthophorini, unlike the Eucerini, are most common and diversified in the Old World (Lieftinck, 1966), but are widespread also in the New World. *Anthophora* is primarily Palearctic, especially abundant in the Mediterranean basin and similar arid warm temperate Palearctic regions, although apparently also widespread in Africa, and rather well represented in North America, including the Madrean region, with a few species reaching the Antilles as well as southern South America. It appears to be rare or absent in much of the intervening American tropics, although present in the Andes. While present in India, it does not occur in Indonesia or farther eastward. *Heliophila* is Palearctic, mostly in arid areas; *Clisodon* is northern Holarctic. In the Old World tropical and south temperate regions (Africa, Southern Asia, Australia, and intervening insular areas eastward to the Solomon Islands) the principal genus is *Amegilla*, which also has a few species in the southern Palearctic. The subgenus or related genus *Asaropoda* is centered in Australia but with a few species extending northward through Indonesia. There is also a series of smaller genera found mostly in warm north temperate, subtropical and northern tropical zones around the world. These are *Deltoptila* in Mesoamerica, *Emphoropsis* in the Nearctic region, *Habropoda* in the Mediterranean region to China, Taiwan, Viet Nam, and India, *Habrophorula* in southeast China, and *Elaphropoda* in the Oriental region, eastward to Java. Finally there is a group (*Pachymelus* and allies) with various Malagasy species but occurring also on the African mainland.

The Melectini consists of bees that are social parasites in the nests of Anthophorini. Not surprisingly, melectine distribution shows similarities to that of Anthorphorini. There are eight genera and subgenera in the Old World. *Melecta* is Holarctic, best represented in the Mediterranean area and eastward in arid parts of Asia. *Thyreus* is widespread in Africa, the southern Palearctic region, the Oriental region, and southeast as far as the Solomon Islands and Australia. Of the remaining Old World genera, one is Oriental, two are east and south African, the rest are Palearctic (Lieftinck, 1972).

There are six genera and subgenera in the Nearctic region, all but *Melecta* s. str. being restricted to western North America. Remarkably enough there is an

additional isolated genus, *Nesomelecta*, in the Greater Antilles. Otherwise the tribe is absent in the American tropics.

The tribe Centridini is largely restricted to the Amercan tropics. *Epicharis* (with nine subgenera) is quite strictly tropical while *Centris* with 12 subgenera (Snelling, 1974) is largely tropical. For both genera the area of greatest abundance and perhaps of diversity is the moist tropics. However, *Centris* extends south into temperate South America (both the Araucanian area and Argentina) and north into the Madrean region and marginally beyond, to eastern Texas, Kansas, etc. Several subgenera occur largely or wholly in these xeric raeas. *Xerocentris* is amphitropical, being absent in the tropics but present in the North American deserts and in the Araucanian area, while *Paracentris* has a similar but somewhat wider distribution; its presence in the Colombian Andes narrows the gap between its northern and southern areas. One of the major groups of the tropics, the subgenus *Centris*, occurs in the Antilles and southern Florida; it also penetrates the Sonoran region.

The tribe Ctenioschelini contains parasites mostly in the nests of Centridini. It is most abundant and diversified in the American tropics, especially Brazil, where six genera occur. One of them, *Mesoplia*, ranges south into temperate South America including Chile, another reaches southern Arizona in the Sonoran region, while two occur in the Antilles. A seventh genus, *Ericrocis*, is restricted to the North American deserts and adjacent areas.

The tribe Rathymini contains only the genus *Rathymus*, found in the American tropics from Mexico to Brazil.

The subfamily Nomadinae consists entirely of social parasites or cuckoo bees whose larvae feed in the cells of other bees. Although in the past there has been some doubt as to whether the subfamily is monophyletic, J. G. Rozen (in litt.) reports additional (larval) characters that support its status as a monophyletic subfamily. Except for one or two species of *Nomada* in northern Australia, the subfamily is absent in that continent, but it is present in all other continents and most diverse in the Americas.

The forms that are parasitic on the Exomalopsini, the closest nonparasitic relatives of Nomadinae, are presumably the most primitive Nomadinae. They are in the tribe Nomadini (including Epeolini and Osirini, which more or less intergrade with Nomadini in South America). The genus *Nomada* is represented from Argentina to Mexico and Cuba by the subgenus *Hypochrotaenia*, parasitic in nests of *Exomalopsis*. The only related subgenus, but more like the typical northern *Nomada*, is *Micronomada*, restricted to the Nearctic region but especially well represented in the desert areas. At least some of its species are also parasites of *Exomalopsis* and perhaps halictids while others probably parasitize *Andrena*. Once this latter habit arose in the Nearctic region, *Nomada* had open to it an enormous trophic and geographic opportunity. The Holarctic distribution of various groups of *Nomada* indicates that the intercontinental dispersal occurred under more mild climates than the present, probably when the Bering Strait area was temperate or perhaps across the North Atlantic in the Paleogene. The inter-American dispersal must have been by island hopping well before the continental union, a probability in view of the presence of *Hypochrotaenia* in the Antilles. In

the Old World, *Nomada*, while common in the Palearctic area as in the Nearctic, has spread with small numbers of species through Africa to the Cape, and through the Oriental region and Indonesia to New Guinea and the Solomon Islands and to northern Australia. There are only a few related species from Indonesia eastward; this distribution must be the result of relatively recent dispersal (and probably on halictid hosts as the area is devoid of *Andrena*). No additional genera related to *Nomada* occur in the Old World but in the New World there are *Osiris*, *Odyneropsis*, *Polybiapis*, and others in the moist tropics (Argentina to Mexico), as well as five additional Nearctic genera (three of them in the deserts, primarily Sonoran) and one Araucanian genus (*Kelita*).

The genera related to *Epeolus* are sometimes placed in a separate tribe, the Epeolini. *Trophocleptria* of the moist tropics (Argentina to Costa Rica) is the most like the nomadine group of genera and through *Pyrrhomelecta* (southern United States to northern South America) grades into *Epeolus*, another holarctic holarctic genus like *Nomada* but a parasite of *Colletes*. *Epeolus* also ranges to southern Africa. *Triepeolus* is another large genus, largely Nearctic and parasitic on a variety of bees, especially Eucerini, but with various species extending through the tropics to southern South America. The few Palearctic species placed in *Triepeolus* are little known but probably are *Epeolus*.

Seven or eight other genera of Nomadini, some like *Thalestria* and *Doeringiella* obviously related to *Triepeolus* and *Epeolus*, others less closely related, are found in South America, largely restricted to the southern Brazilian to Argentinian part of the continent.

Other tribes of the subfamily Nomadinae are mostly smaller and more restricted in distribution. Thus the Epeoloidini (one genus, *Epeoloides*) is Holarctic. The Protepeolini range from temperate South America to the North American deserts. The genus *Protepeolus* has two species, one in the North American deserts (south to Guatemala), the other in the arid parts of central Argentina (Eickwort & Linsley, 1978). Another genus (*Leiopodus*, only tentatively included in the tribe) is tropical American. The Isepeolini (one genus, *Isepeolus*) occurs from temperate Brazil to Argentina and Chile.

The remaining tribes of Nomadinae are the mostly small "pasitine" bees, as a whole better represented in the Old World than in the New World. Their relationships to other Nomadinae are not clear but recent studies support their inclusion in that subfamily (J. G. Rozen, in litt.).

The tribe Caenoprosopidini contains a single genus (*Caenoprosopis*) and species found from southern Brazil to Argentina.

The Neolarrini and Townsendiellini are Nearctic, largely restricted to xeric areas. Only three genera and subgenera are involved. The Ammobatini are most diverse in Africa (6 genera) including Madagascar (which has an endemic genus as well as an African genus) but three genera range into or are largely restricted to the Palearctic region and one (*Oreopasites*) is found in the western United States.

The tribes Holcopasitini and Biastini each contains two genera, one Nearctic, one Palearctic. The tribe Ammobatoidini contains a single genus whch is Palearctic.

The last anthophorid subfamily is the Xylocopinae. While a few species of the subfamily occur in Mediterranean climates or even desertic areas, the only groups limited to such areas are *Proxylocopa* and *Manuelia.* The tribe Xylocopini contains the large carpenter bees, most of which nest in wood or coarse stems. It is primarily tropical and subtropical in both hemispheres, with a few groups and species penetrating well into the temperate zones. The diversity of the group is greatest in the Eastern Hemisphere. There is a ground-nesting Mediterranean to central Asian genus (*Proxylocopa*) and an Australian genus (*Lestis*) in addition to the widespread *Xylocopa.*

The latter genus has been much subdivided. It is abundant in the moist tropical as well as in drier tropical and subtropical regions. In the Americas there are 17 subgenera. Most are Neotropical, being especially numerous in the area of southern Brazil to Argentina; two primarily Neotropical subgenera reach the southern United States and one of them is in the Antilles also. Two of the 17 subgenera are Nearctic, extending into the northern Neotropics, and one is Mesoamerican. None occurs in the Araucanian region. There is no special abundance of *Xylocopa* in the Madrean area and no species are restricted to that area.

In the Old World there are 31 subgenera. Fifteen of these occur in Africa, a few of them also being in India and southeast Asia, and one, *Koptortosoma*, ranges from Africa to the Philippines and through Indonesia to New Guinea and Australia. There are no other groups of *Xylocopa* in Australia. Unusual for bees, *Xylocopa* has 11 subgenera restricted to the Oriental Region, some found only or principally in southeast Asia and three restricted to Indonesian islands. Three subgenera are primarily Palearctic and several others enter the Palearctic region slightly in India, China, or the Mediterranean basin.

No subgenus occurs both in the Americas and in the Old World. However, there are some relationships that suggest several dispersals perhaps across the North Pacific. Thus the Palearctic *Xylocopa* s. str. resembles the Nearctic *Xylocopoides*, the Chinese *Mimoxylocopa* resembles *Stenoxylocopa* which ranges from Argentina to Arizona, and the Palearctic (and African) *Rhysoxylocopa* resembles *Notoxylocopa* of the western United States (and south to Colombia). The other major disjunctions are those which occur in the African-Oriental subgenera which skip from Africa to India. The Malagasy *Prosopoxylocopa* is related to the Oriental *Zonohirsuta*, not to African subgenera.

The other tribe of the subfamily Xylocopinae is the Ceratinini, or small carpenter bees. The genus *Manuelia* contains three species, each very different from the others, perhaps at a generic or subgeneric level, and all restricted to the Araucanian region. This is probably an archaic genus; it has no close relatives elsewhere. *Ceratina* is a large genus, abundant on all continents except Australia which has only one species which is similar to forms found in India and intervening regions. The genus has been divided into a dozen or more subgenera (Michener, 1954; van der Vecht, 1952) but as no worldwide study has yet been made, the biogeography of the subgenera is not clear. In particular, the rich African fauna has received little classificatory attention. There is no evidence of major disjunctions, nor of close relationships between groups of the southern continents. As with *Xylocopa* and unlike most groups of bees, there are a number

of Oriental groups (*Chloroceratina, Catoceratina, Lioceratina, Xanthoceratina, Ceratinidia, Pithitis*) most of them restricted to southeast Asia and major continental islands. *Ceratinidia* and *Pithitis* range across Indonesia to New Guinea and the latter has a single species in Africa. While its dispersal southeast from Indonesia is very limited (2 species, one reaching the Solomon Islands, the other reaching middle latitudes in eastern Australia), *Ceratina* extends far across the Pacific farther north, having an endemic species in Micronesia (Krombein, 1950). *Ceratina* includes about six subgenera in the Americas, only one of them primarily Nearctic, the others either restricted to or best developed in the Neotropical region. There are species in the Antilles.

The remaining Ceratinini constitute a group commonly called the allodapine bees (Michener, 1977). Their center of abundance and diversity is Africa, where there are ten genera and subgenera. Six of these taxa are restricted to southern Africa, which thus has greater diversity than any other area (Michener, 1975). One major African genus, *Braunsapis*, also occurs in southern Asia and east as far as Taiwan, the Philippines, Solomon Islands, and the northern half of Australia. Another extends beyond Africa only to the Arabian Peninsula. There is also a monotypic genus (*Exoneuridia*) restricted to Asia Minor. It is the only north temperate allodapine genus, although *Braunsapis* enters temperate climates marginally in Asia. The African genera *Macrogalea* and *Halterapis* as well as *Braunsapis* are found on Madagascar, where there is also another genus, *Effractapis*, derived from *Braunsapis*.

Four additional genera and subgenera, *Exoneura* and its relatives, occur in Australia. All are restricted to temperate parts of the continent and one of them reaches Tasmania.

Those allodapines that have the largest number of ancestral characters (characters in common with *Ceratina*) are African. The group may well have originated there and spread thence over the rest of the Old World tropical and south temperate regions. *Braunsapis* presumably arrived in Australia from the north by way of the islands, among which it has shown a good dispersal ability. The way has been open, more or less as at present, for 15 m.y. The *Exoneura* group of genera presumably reached Australia earlier, and either was to begin with or became, adapted to temperate climates.

To summarize for the Anthophoridae, it seems likely that the initial radiation was in South America, probably after that continent was more or less isolated. This radiation involved the Exomalopsini and various groups probably derived from it like the Tetrapediini, Melitomini, Eucerinodini, Canephorulini, Eucerini, Centridini, Ctenioschelini, Rathymini, as well as the subfamily Nomadinae. Of these only the Exomalopsini-Ancylini, perhaps with the Pararhophitini, the Eucerini, and the Nomadinae reached the Old World, principally the Paleartic, probably via North America, but several of the other groups penetrated into North America. The Anthophorini and Melectini are predominantly Old World groups whose relationships to the New World groups are not clear. They are probably ultimately derivatives of Exomalopsini or similar bees. The radiation of the Xylocopinae has been primarily tropical, in both eastern and western hemispheres. The most primitive genus of Xylocopini, however, is the Mediterranean to central Asian

Proxylocopa. Useful speculation as to areas of origin and initial radiation for both Xylocopini and Ceratinini seems premature.

APIDAE

This family, which includes all the highly social bees as well as others, has, for that reason and because of the apparently specialized pollen-carrying corbicula, usually been considered as the most specialized of the long-tongued bees. However, the distribution of what is presumably the oldest group (Meliponinae, the sister group of all the other Apidae according to Winston & Michener, 1977) exhibits discontinuities that may indicate greater antiquity than for surviving groups of other long-tongued families except the Fideliidae.

The Meliponinae or stingless honeybees are pantropical, richly represented in the wet tropics and usually less abundant in other tropical areas, extending into the temperate zone in the southern continents but not or scarcely in the northern ones. Before general acceptance of continental drift, I believed that the intercontinental tropical discontinuities of Meliponinae, different from any other bee distributions, indicated an ability to traverse oceans rarely as nests in hollow trunks. Their food stores and known ability to survive imprisonment in their nests made this hypothesis seem reasonable. However, the Meliponinae seem actually to be poor at dispersal across water. In spite of a rich continental fauna there is only one extant Antillean species and it is the same as the principal domesticated species of *Melipona* in Yucatán. It is likely that it was carried to the Antilles by primitive man. There are few Malagasy species, all closely related to African forms of the genus *Trigona*, subgenus *Hypotrigona*. Only in the east Asian and Indonesian area is there evidence of considerable island-hopping, for species of the subgenus *Tetragona* are found in the Philippines and throughout Indonesia and beyond to the Solomon Islands and Australia. Most of the *Tetragona* species east of the islands recently joined with Asia belong to a single small group of closely allied species called by Moure (1961) *Tetragonula*. Perhaps this group possesses some attributes that make over-water transport more likely than for other groups. Krombein (1950) attributes the presence of two species in Micronesia to man. In any event, it now seems probable that for most Meliponinae, oceans have not been traversable; the disjunct distributions are probably explicable in part on the basis of plate tectonics.

The Meliponinae have been much subdivided (Moure, 1961) but the 19 genera and subgenera recognized by Wille (in preparation) are more instructive than finer subdivisions for biogeographical studies. There exist three main groups: *Melipona* in tropical America (Argentina to Mexico), *Meliponula* (in spite of its name not closely related to *Melipona*) with a single widespread tropical African species, and the group of *Trigona* and its allies (including *Lestrimelitta* and *Dactylurina*) in all tropical continental areas. The latter group is by far most diverse in tropical America, where there are 14 genera and subgenera. Among the American forms are the subgenera *Trigona* s. str., *Trigonisca*, *Tetragona*, and *Plebeia* of *Trigona*, all with many species, and the genus *Lestrimelitta* containing two species of robber bees that never visit flowers but forage in the nests of other

Meliponinae. All American subgenera of *Trigona*, as well as *Lestrimelitta*, are rather widespread, at least from Brazil to Costa Rica, and most from northern Argentina to Mexico. In southern Brazil and adjacent countries there are three or four distinctive species or species groups of *Trigona* not found elsewhere. No such unusual forms occur near the northern limit of the stingless bees' range in Mexico. No meliponines reach the Araucanian area, and no members of the *Trigona* group now occur in the Antilles, although as indicated elsewhere, fossils of the subgenus *Hypotrigona* have been found in Hispaniola.

The *Trigona*-group of Africa comprises only five genera and subgenera. Two of these, *Meliplebeia* and *Axestotrigona*, are strictly African. The others show noteworthy similarities to Neotropical forms. *Hypotrigona* of Africa is closely related to the Neotropical *Trigonisca*. There are several species of *Plebeia* differing from those of the Neotropics in having a larger and presumably ancestral (but nonfunctional for stinging) sting apparatus. There are no *Tetragona* species in Africa but a single species placed in the separate genus *Dactylurina* is nothing but an unusual *Tetragona*. Finally, the African robber bees are placed in *Cleptotrigona*, which may be related to the American robber genus *Lestrimelitta* or may be independently derived from flower-visiting *Trigona* (*Hypotrigona*) species in Africa.

The *Trigona* of southern Asia, although much more numerous in species and individuals, especially in southeast Asia, than in Africa, all belong to three subgenera. One is tentatively considered as *Hypotrigona*, the same subgenus as those of Africa. Another is *Lepidotrigona*, found only from India to Java and Borneo. The third, a large group in the Oriental area, is *Tetragona*. It contains numerous subgroups and many species, and ranges from Sri Lanka and India to Borneo and Java with one species group extending onward to the Philippines, Solomon Islands, and south to the northern half of Australia. None of the Oriental species groups is the same as those of the Americas, but the presence in both continents of forms of *Tetragona* with and without sericeous hind basitarsal areas suggests at least two intercontinental dispersals. Repeated detailed studies (Wille, 1977) show no consistent differences between Oriental and Neotropical groups of *Tetragona*.

Finally, in the north half of Australia and in New Guinea, in addition to the *Tetragona* mentioned above, there exist species of the subgenus *Plebeia* similar to those of the Americas, lacking the primitive features of the African *Plebeia* species.

The *Trigona* species from the Eocene Baltic Amber cannot be placed in any of the modern subgenera and apparently constitutes an undescribed subgenus. *Trigona silicea* from Oligomiocene amber in Chiapas, Mexico, is a member of the small Neotropical subgenus *Nogueirapis*, a relative of the subgenus *Plebeia*. Thus at least the more primitive extant groups were in modern form by the beginning of the Miocene. The most interesting fossil is *Trigona dominicana* from Oligocene (?) amber of the Dominican Republic (Wille & Chandler, 1964). It demonstrates that the *Trigona*-group once occurred in the Greater Antilles, although now extinct there. Moreover, it is a *Hypotrigona*, a subgenus not now found in the Americas although present in Africa, Madagascar, and southeast Asia.

Since at least three transatlantic dispersals would be necessary to explain the

disjunctions described above (for *Plebeia*, *Tetragona*, and *Hypotrigona-Trigonisca*), fortuitous transport seems unlikely. It is more likely that the principal subgenera of *Trigona* originated in the middle or upper Cretaceous when Africa and South America were joined or not yet widley separated in tropical latitudes (see Förster, 1978).

The subfamily Bombinae contains two very different tribes. The Euglossini consists of about eight genera and subgenera, all found in tropical Amercia. The major genera (*Euglossa, Eulaema, Euplusia*) range from northern Argentina to Mexico; others, especially *Aglae,* are limited to the Amazon or similar forests. One species of *Euglossa* occurs in Jamaica; otherwise the tribe is absent in the Antilles.

The tribe Bombini consists of two genera, *Bombus* and *Psithyrus*, the latter parasitic in nests of the former. The tribe is primarily holarctic, and most abundant in cool temperate zones, but species of *Bombus* range essentially as far north as there is land in the arctic as well as to Tierra del Fuego in the south, thus into colder climates than are inhabited by any other bees.

Psithyrus is restricted to the Holarctic region. *Bombus* is divided into 35 subgenera (Richards, 1968). Of these five are Holarctic and 17 Palearctic, so that 22 occur in the Palearctic region, the area of greatest diversity. By contrast, there are only five Nearctic subgenera (one of them also Neotropical), making a total of 10 in the Nearctic region. Five subgenera occur in South America, mostly in Andean and southern regions, although two species exist in the Amazon Valley. One Holarctic subgenus extends into southeast Asia and there are three other Oriental subgenera, all montane, one extending as far southeast as the mountains of Java. The genus is probably absent in sub-saharan Africa. A single queen of an American subgenus has been described from Guinea (Tkalců, 1966), but it is likely to represent an introduced or possibly mislabeled individual.

The subfamily Apinae contains only the genus *Apis*. Prior to dispersal of *A. mellifera* by man, the genus was restricted to the Oriental, Palearctic, and African regions. The greatest diversity is in the Oriental region. While it occurs in Taiwan and the Philippines, the genus does not reach New Guinea or Australia. One species, *A. cerana,* ranges from southern Asia to Palearctic China and Japan. Another, *A. mellifera*, ranges from western Asia throughout Africa (including Madagascar) to the Cape and north in Europe as far as southern Norway. Except for these two species, the genus is tropical and subtropical, and Oriental. Obvious members of the genus occurred, however, in Europe in the Oligocene (Zeuner & Manning, 1976), as did the extinct apine genus, *Electrapis*, in the Eocene.

To summarize for the Apidae, the Meliponinae are apparently an ancient tropical group that arose and radiated in the former West Gondwanaland when Africa and South America were much closer than at present. The subfamily is now best represented in South America. The Bombinae may have had a similar origin, for the Euglossini are strictly Neotropical, but the Bombini entered cool temperate climates and radiated primarily in the cool Palearctic region. The origin of the Apinae is obscure, but it is now centered in the Oriental region, occurring also in the African and Palearctic areas, and was in the last mentioned as early as late Eocene.

Disjunctions

The distributions of most bee taxa are not disjunct or, if so, are limited to neighboring continents and could have been attained with the continents in their present positions. Some taxa are found in most or all continents and even many islands, and obviously have considerable potential for traversing major water barriers. Probably the dispersal of some such groups preceded the present arrangement of the continents, but when we lack knowledge of the cladistics within a taxon (e.g., of subgenera within a genus), no conclusions can be drawn as to the time and manner of the major dispersal. Numerous taxa, by occurring on both sides of a major physiogeographic or climatic barrier, provide some information on their antiquity or dispersal ability.

The very many Holarctic taxa are all disjunct. Those that occur in boreal environments may be scarcely so, however, and there are a few Holarctic species (in *Andrena*, *Halictus*, *Osmia*, *Formicapis*, *Clisodon*, *Bombus*) that presumably crossed the Bering Strait area sufficiently recently that obvious or species-level differentation of North American and Eurasian populations has not occurred. Most bees, however, require warmer climates than those now found in the Bering Strait area; intercontinental disperal was therefore older and Eurasian and North American populations are mostly at least specifically distinct.

Some taxa or groups found in both northern continents and not occurring north of the more or less warm temperate zone are the following: *Nomia* (2 groups), *Panurginus*, *Macropis*, *Diceratosmia*, *Chalcosmia*, *Chelostoma*, *Heriades*, *Trachusa*, *Anthidiellum*, *Xenoglossodes*, *Melecta*, Holcopasitini, Biastini, *Xylocopa-Xylocopoides*, *Mimoxylocopa-Stenoxylocopa*, *Rhysoxylocopa-Notoxylocopa*. Probably most of these groups traversed the Bering Strait area. Restriction of several of the groups (*Chelostoma*, *Trachusa*, Biastini, *Notoxylocopa*) in America to the west suggests this route. Others, such as *Nomia* and *Melecta*, are principally western in North America. Certain of the forms listed, however, are largely eastern in their American distributions (*Macropis*, *Diceratosmia*). This limitation might result from the current climate, but also suggests dispersal across the north Altantic, a route which was open for plants throughout the Tertiary (Raven & Axelrod, 1974), although becoming less and less practical as North America and Europe moved apart.

Many organisms inhabit Mediterranean and desertic climates of both North and South America and are absent from the intervening tropics. These amphitropical distributions have long been a subject of interest (Raven, 1963, 1972; Raven & Axelrod, 1974). Among the bees, none involves specifically the Californian area of Mediterranean climate, nor are there polar (boreal) amphitropical bees. In North America most amphitropical bees are primarily Sonoran and Chihuahuan desertic elements, although *Caupolicana*, *Protandrena*, and *Ptilothrix* each has an eastern North American species or two. Other amphitropical taxa (Andreninae, Dufoureinae, and *Calliopsis* and allies) are wide ranging in North America. In South America, amphitropical bees occur either in the Argentina-southern Brazilian area, often in its more xeric parts, or in the Araucanian region. The following lists of amphitropical taxa show that only *Calliopsis* and its relatives

and *Protandrena-Psaenythia* occur in both. (*Protandrena* and *Psaenythia* are listed in this paragraph by virtue of their close relationship to one another; each is restricted to its continent but they constitute an amphitropical group.)

Amphitropical groups occurring in Argentina-southern Brazil: *Eulonchopria*, *Zikanapis*, *Protoxaea* s. l., *Protandrena-Psaenythia*, *Calliopsis* and relatives, *Dasiapis*, *Ptilothrix*, *Martinapis*, *Protepeolus*.

Amphitropical groups occurring in the Araucanian region: *Caupolicana* s. str., Dufoureinae, Andreninae, *Protandrena-Psaenythia*, *Calliopsis* and relatives, *Xerocentris*.

Certain other tentatively amphitropical or almost amphitropical groups are listed in the preceding section.

Dispersal between the savanna, grasslands, macchia, and deserts of South America and similar arid environments of North America must have been greatly facilitated by aridity in the tropics during the Pleistocene. In some cases (especially the Dufoureinae and Andreninae), however, the South American forms are quite different from any North American ones and dispersal must have been much earlier. As there is no evidence for an arid corridor during the Tertiary (or at any other time), long distance dispersal probably accounts for such distributions, perhaps facilitated by local xeric areas as suggested by Michener (1954). The elevation of the Andes progressively increased the possibility of intercontinental dispersal by creating cool or arid habitats near the equator. There is an alternative to long distance dispersal, however. From time to time in its history a xeric-adapted genus may give rise to a species able to exist in mesic or humid habitats. For example, *Ashmeadiella*, a generally xeric-adapted genus, has one species that ranges eastward in North America as far as Indiana and Georgia and another that occurs from North Carolina to Florida. Should such a species reach another xeric area, it might well speciate there, and if it then disappeared in the intervening mesic area, one could have a cluster of species in each xeric area and a problem in explaining how the genus traversed the mesic area.

The direction in which amphitropical groups spread is sometimes not obvious. However, it is probable that *Penapis* (Dufoureinae) and *Euherbstia* and *Orphana* (Andreninae) originated in the north while *Eulonchopria*, *Zikanapis*, *Caupolicana* and probably most of the rest originated in the south.

In the Old World, many tropical groups occur in Africa, and then again from Sri Lanka and India eastward across southern Asia, often with little differentiation between forms in the two areas. A more humid (not wet tropical but savanna) climate across the Arabian peninsula, southern Iran, and west Pakistan would connect or nearly connect these areas for the bees concerned, even with the continents in their present positions. Since more humid conditions undoubtedly existed in this area in the not very distant past, this disjunction, like that for cool temperate forms across Bering Strait, is easy to understand. Some of the taxa involved are *Thrinchostoma*, *Pachyhalictus*, *Ctenoplectra*, *Creightonella*, two or more subgenera of *Chalicodoma*, various subgenera of *Xylocopa*, and *Braunsapis*. Certain others may have crossed from Africa to southern India directly or via islands, and have not extended farther eastward. Such forms are *Eupetersia* and *Eucara*. There is nothing to indicate that any aspects of modern bee distribution

in the Indian Ocean area depend upon movements of Madagascar or India. Any bees which were in India when it moved across the Indian Ocean are lost or have dispersed widely (possibly like *Hylaeus*) and become unrecognizable as such.

Most of the taxa having an African-Oriental distribution have their centers of diversity in Africa. The reverse is true for *Pachyhalictus*, *Pithitis*, *Apis* (the last two with only 1 African species each), and for *Hoplonomia* and the *Prosopoxylocopa-Zonohirsuta* group of *Xylocopa*, which reach Madagascar but not Africa proper.

For some groups the island-filled sea between Asia and Australia is only a partial barrier. Before the Miocene (about 15 m.y. BP) the sea was broader, probably without large islands, and accordingly was an effective barrier. Various groups of bees occur both in Asia and Australia, as well as intervening islands. Such distribution is found in *Homalictus* (probably an old Australian genus that spread to Asia) and in *Lasioglossum* s. l., *Sphecodes*, *Nomioides*, various subgenera of *Nomia* and of *Chalicodoma*, *Amegilla*, *Braunsapis*, *Tetragona*, and others (all of which appear to have spread from Asia to Australia). In some cases Asiatic and Australian species are very similar, indicating recent spread across the ocean barriers.

The remaining disjunctions to be discussed are probably all old, perhaps resulting from or exaggerated by continental movements that occurred during and since the Cretaceous. The bees involved (with the possible exception of *Chelostomoides-Hackeriapis* and the Meliponinae) seem to be archaic types, and the taxa may have been parts of the initial rapid radiation of the bees. Except for the Meliponinae, all the taxa discussed below are largely inhabitants of xeric areas; the Fideliidae and the *Hesperapis* group are limited to such areas. Thus the importance of xeric environments as habitats for primitive bees is reemphasized.

The Paracolletini are found principally in temperate parts of Australia, South America, and Africa and the Fideliidae in desertic parts of Chile and South Africa. Dispersal between Australia and South America through cool temperate Antarctica would have been possible as recently as the beginning of the Oligocene (38 m.y. BP). This route could perhaps have been traversed by the paracolletines. Connections to Africa were disrupted earlier; by the end of the Cretaceous, while relatively narrow seas separated tropical Africa and South America, temperate parts of these continents were already well separated. Thus the Fideliidae and perhaps the Paracolletini may have originated as long ago as the Upper Cretaceous. (As indicated elsewhere, however, long distance transoceanic dispersal could explain the Afro-Australian or Afro-American disjunctions of Paracolletini and Fideliidae, respectively.)

Dispersal among xeric areas outside the southern hemisphere also presents difficult problems. The primarily Australian-North American distribution of the *Hackeriapis-Chelostomoides* group of *Chalicodoma* has been discussed elsewhere. (*Hackeriapis* is Australian, north to New Guinea savannas; *Chelostomoides* is North American, especially Madrean, south to Colombia.) Long distance dispersal seems unlikely from Australia to North America. The Bering Straits would seem a likely route, but if it were used, why is the nearest relative of

Chelostomoides in Australia instead of in Asia? Alternatively, dispersal from Australia to South America through cool temperate Antarctica would have been possible in the Paleogene, but if this route were used, what happened to the group in most of South America, some of which is climatically and vegetationally so similar to the desertic areas of North America where *Chelostomoides* is abundant and diversified?

The *Hesperapis* group of genera (South Africa, Central Asia, and the Madrean and adjacent areas) also occurs in deserts of both the Northern and Southern Hemispheres. It may have originated in arid parts of Africa, as suggested by the presence of related melittids there, and during dry epochs extended to the Mediterranean-Central Asian arid zone. Certain other bees have such distributions, and *Poecilomelitta* ranges from arid southern Africa to Iran, without entering the Mediterranean basin. The unusual feature of the *Hesperapis* group's distribution in the Old World is its absence between Central Asia and South Africa. It probably became extinct between these areas; there is no need to postulate long distance dispersal. The problem is, how did it get to the New World? The Exomalopsini-Ancylini may have spread from arid parts of North or South America to the Mediterranean region. The Old World forms are mostly in arid areas, as are some Exomalopsini. Moreover, the similarities of such bees as desert *Hoplitis* (and related genera) and desert *Anthophora* (subgenus *Micranthophora*) of the Madrean area to those of the Mediterranean-Central Asian area may not be convergent, but may possibly result instead from common ancestory. Further studies are needed to determine the cladistic relationships. In any case, at least some bees moved between the Old World and New World dry areas. Raven & Axelrod (1974) suggest that eastern North America and western Europe were in latitudes suitable to warm, seasonally dry climates in late Cretaceous and early Eocene, and were separated by only moderately broad seas. If so, bees of dry areas could have been exchanged more readily than under present conditions, but probably only by long distance dispersal as emphasized by Raven (1972).

The disjunctions noted previously for Meliponinae are unique among bees in that they involve a group characteristic of the moist tropics, and except for one subgroup, with minimal ability to cross water. The disjunctions are indicated as follows:

Plebeia—American tropics, Africa, Australia and New Guinea.
Tetragona—American tropics, Africa (related *Dactylurina*), Oriental region to Australia.
Hypotrigona-Trigonisca—American tropics, Africa, Oriental region.
Lestrimelitta (if monophyletic)—American tropics, Africa.

The genus *Trigona* was present in Europe in the Eocene (Baltic amber) (Kelner-Pillault, 1970); it probably dates from before that time, and some modern subgenera such as *Plebeia* from not much later. Raven & Axelrod (1974) indicate that Madagascar and India might have served as a subtropical migration route between Africa and Australia until near the end of the Cretaceous (see their Fig. 2). If *Plebeia*, which is among the most primitive Meliponinae, reached Australia at that time and disappeared from India as it became dry during its

movement toward Asia, the absence of *Plebia* in Asia and its presence in Africa, Australia and New Guinea could be explained. The South American-African connection was severed in earlier Upper Cretaceous, suggesting an antiquity for *Plebeia* of 65 to 100 m.y., that is, an origin for the subgenus in the Upper Cretaceous. This seems unlikely in view of the probable time of origin of the bees; dispersal across a narrow Atlantic seems more likely; in tropical latitudes the Atlantic remained narrow for a long time (Förster, 1978). Perhaps *Tetragona*'s occurrence both in the Old World and in the Neotropics can be explained in the same way. *Tetragona* may have spread in the Old World relatively recently, becoming extinct, except for the derived *Dactylurina*, with drying and elevation in Africa. *Hypotrigona-Trigonisca* is a primitive group whose trans-Atlantic dispersal could be explained as for *Plebeia*.

Comparison of Faunal Regions

A rough comparison of bees in faunal regions can be obtained by comparing the columns in Table 3. The last row in that table gives the numbers of tribes, subfamilies, and families found in each faunal region. This is one measure of faunal richness or poverty. Another is the number of genera and subgenera found in each region, as follows:

Australian—127	Neotropical—315
African—175	Nearctic—260
Oriental—89	Palearctic—243

The above figures are based on numbers which for different groups in different areas are mere estimates. Thus for a genus that has been well revised and divided into meaningful subgenera in certain continents, I have estimated (or made a guess at) the probable number of subgenera in other continents where appropriate studies have not been made. Moreover, I have omitted some genera or subgenera that enter a certain area only marginally. For example, the widespread Neotropical genus *Pseudaugochloropsis* is not counted in the Nearctic region although it has been taken near Brownsville, Texas.

In the following paragraphs attributes of the fauna of each faunal area are described. To avoid duplication, I have not usually repeated below, but have merely referred to, the information on disjunct distributions contained in the preceding section. Ideally, for any area, one ought to be able to indicate which taxa originated in that area, and which entered it, and when, from which other areas. In the almost complete absence of a useful fossil record, one is largely dependent upon present distributions and surmises as to past climates and continental connections. I have made this section brief by omitting many purely speculative considerations.

Australia is the only continent where a high percentage of the taxa (64% of the genera and subgenera, nearly half of the species, Michener, 1965a) belong to the primitive family Colletidae. Presumably this results from the long isolation of the continent, from the time of its separation from the rest of Gondwanaland at the end of the Eocene until its present broken connection with Asia devel-

oped in late Miocene. It probably preserves something resembling the temperate Gondwanaland bee fauna, infiltrated by various other types.

Aside from the colletids, only *Hackeriapis* in the Megachilini (relatives in North America) and *Plebeia* in the Meliponinae (also in Africa and the Neotropics) among Australian bees show major disjunctions. Other groups all could have reached Australia from Asia at various times during Australia's approach to that continent. Ancestors of the *Exoneura* group (Ceratinini) and of some halictids, especially *Homalictus* and *Austronomia*, however, probably arrived early, possibly via southern connections. Thus all these groups also could have been part of the Gondwanaland bee fauna. Absence in South America of bees related to the halictids and Ceratinini mentioned above may suggest that they were early transoceanic arrivals. It must be remembered, however, that Australia and South America were never in contact but were joined by Antarctica, a large continent whose effectiveness as a faunal bridge was limited in the early Tertiary to forms able to tolerate cool temperate climates. For warm-temperate organisms this bridge probably failed about 100 m.y. BP, before the middle of the Upper Cretaceous.

Most of the large Australian bee fauna inhabits the dry temperate region, and is dependent on Myrtaceae for pollen and nectar (Michener, 1965a). Australia is the only continent where one family of plants has a pre-eminent position as a food source for bees. These bees are not well represented, although present, in cool temperate areas; only 20 genera and subgenera occur in Tasmania.

The typical Australian groups are surprisingly poorly represented in the Australian rainforests, in New Guinea and nearby islands, and even in the dry savannas of tropical northern Australia. Various Australian groups do occur, however, in northern Australia and New Guinea, and a few (*Palaeorhiza*, *Homalictus* and certain subgenera of *Nomia*) are unusually developed in New Guinea. A few taxa from Asia enter this region (New Guinea and northernmost Australia) but not temperate Australia; *Pachyhalictus*, *Ctenoplectra*, *Chelostomoda*, and *Pycnanthidium* are examples. In fact, if one ignores the Australian elements, the fauna of northern Australia, New Guinea, and the Solomon Islands is a depauperate extension of the Oriental fauna, which is itself a depauperate extension of the African fauna. Thus there is a single paleotropical bee fauna, richest in Africa and progressively reduced to the east.

New Zealand and New Caledonia have the smallest bee faunas of any substantial land areas of the world. New Zealand has only four native genera and subgenera; species are also few. These islands have no unusual genera or higher categories that might have been there since these land masses were isolated in the Upper Cretaceous, 80 m.y. BP. If these lands had bees at that time, they must now be extinct. The few bees on the islands today are all congeneric with Australian forms, and all but a few New Zealand species of *Leioproctus* are in the same subgenera as Australian species. Thus the entire fauna appears to have arrived relatively recently over the water.

Sub-Saharan Africa (for simplicity usually called "Africa" in this paper) has a rather rich tropical bee fauna. Nomiinae, Megachilini, various halictids, Xylocopini, and Ceratinini are especially well represented, and for Nomiinae, Mega-

chilini, Xylocopini, Ceratinini, Ammobatini and Ctenoplectrinae, this is the center of diversity. Some large groups of Halictini such as *Zonalictus* and *Thrinchostoma* are either restricted to or centered in tropical Africa. Some or all of the groups listed above may have originated in Africa. There is no evidence that they originated prior to the break up of Gondwanaland, although the representation of the Nomiinae, Megachilini, Ceratinini (*Exoneura* and relatives) and also the subgenus *Plebeia* in the Meliponinae in Australia suggests that these groups might date to that time. More likely most of these groups merely crossed narrower oceans than those that now separate these continents. The good representation of *Xylocopa* and *Ceratina* in South America might suggest the same thing.

Africa was connected to or very near Eurasia until the Paleocene (about 63 m.y. BP) and again since the Miocene (about 25 m.y. BP). Thus faunal interchange with the Palearctic (which region now includes the north African coast) has long been possible, and there is no good evidence as to which tropical African groups originated there and which came from Eurasia (southern European parts of which once had tropical climates). The continental limits have not coincided with the climatic limits and plants and insects have, to a certain degree, been able to ignore the former.

Africa is surprisingly lacking, so far as known, in xeric-adapted forms along the southern margin of the Sahara, but various tropical genera exist in the east African savanna and into Ethiopia and Somalia. Some primarily tropical groups like Nomiinae and *Xylocopa* are represented not only in the marginally tropical areas but also in the Mediterranean basin and southern Europe.

The tropical African forest fauna is sparse compared to that of South America, possibly because of the more severe results of tropical aridity, as well as because of lack of a large south temperate source area and the persistent oceanic, savanna, or desert barrier to the north. Among bees, there is no evidence of widespread extinctions in Africa. There are no groups of bees found in South America and Madagascar or South America and southeast Asia, but absent in Africa, a well known distributional pattern in plants (Raven & Axelrod, 1974). This is not surprising considering that bees generally do well in dry areas, and the only partial exception is the subgenus *Tetragona* of the Meliponinae, represented in Africa only by a specialized derivative, *Dactylurina*. The meliponines, unlike most bees, are primarily insects of tropical moist forests. The meliponine fauna of Africa is the smallest of any major tropical area, although some of the species are in some features the most primitive extant members of the subfamily. Certain Palearctic forms such as *Andrena*, the Dufoureinae, the subgenus *Seladonia* in the Halictini, some megachilid taxa including *Hoplitis*, and probably the African groups of Panurginae, range south through east Africa and enrich not only the equatorial African fauna but that of the Cape region.

Other continents, of course, also have contributed to or received elements from tropical Africa. As noted below in the discussion of the Oriental region, a few taxa centered in that area enrich the African fauna, although for most bee groups Africa has the richer and the Orient the more depauperate representation. South America and Australia show special relationships to tropical Africa only in the Meliponinae.

The *Cape region of South Africa*, including most of Cape Province, has a distinctive bee fauna, most elements of which also occur in the more mesic parts of southern Africa like Natal. This fauna lacks many elements of the tropical African fauna (although including some, such as the allodapines *Allodape* and *Braunsapis* and the halictid genus *Zonalictus*), and it is characterized by a number of other groups, some of them presumably archaic. The Melittinae and Dasypodinae are better represented and more diverse in southern Africa than elsewhere and the following are restricted to that region: the paracolletines *Scrapter* and *Parapolyglossa*, the fideliids *Fidelia* and *Parafidelia*, the halictid *Patellapis*, an undescribed genus of Hylaeinae, and the allodapines *Halterapis* and *Allodapula*. As noted elsewhere, some of these taxa probably had Gondwanaland origins and date to early apoid radiation. Thus the paracolletines are otherwise Australian and temperate South American, the Fideliidae are otherwise Araucanian, and the Hylaeinae may suggest an Australian connection. Certain forms of Palearctic origin, such as *Andrena* and the Dufoureinae, as noted above, also occur in the Cape region, but none has speciated to produce a large south temperate group or complex in Africa.

While the Cape region has a rich and interesting bee fauna, there is no counterpart to its enormous flora (Axelrod & Raven, 1977). Bee species are seemingly less numerous on the Cape Peninsula than somewhat to the interior, and there is none of the fantastic speciation that has occurred in plant genera, e.g., *Erica*.

Madagascar has a few distinct genera such as *Parathrincostoma* and *Effractapis*. Its fauna has been poorly studied and there are probably others to be recognized. However, there is no evidence of archaic types that might have been isolated there when Madagascar separated from Africa in the Upper Cretaceous, nor is there evidence of survivors there of formerly widespread taxa that may have become extinct in Africa. The fauna has been accumulated from repeated transoceanic dispersals, mostly from Africa but with a few taxa (e.g., *Hoplonomia*, *Prosopoxylocopa*) from the Oriental region.

The *Oriental faunal region* includes areas of both Gondwanaland (India) and Laurasian origin, and for purposes of bees, should perhaps be considered to extend as far east as New Guinea, which is also largely of Gondwanaland origin. The Oriental region has the poorest tropical bee fauna in the world (except that of Northern Australia and New Guinea) in spite of the fact that it is the richest area in the world in endemic primitive angiosperms. To a major extent it is inhabited by a depauperate African bee fauna. The section on DISJUNCTIONS lists some of the African taxa that also range from India eastward across southern Asia and indicates how they probably reached Asia from Africa. Some taxa, such as *Eupetersia* and *Eucara*, only reach India, while most (*Thrinchostoma*, various Nomiinae, *Ctenoplectra*, *Creightonella*, *Braunsapis* and various subgenera of *Megachile*, *Chalicodoma*, and *Xylocopa*) extend eastward at least to the Asiatic continental islands and some beyond, as far as New Guinea, the Solomon Islands, and even northern Australia. Perhaps the periodic arid epochs have benefited the tropics elsewhere (especially in the Americas) as bee habitats and led to much speciation and evolution on tropical faunas, whereas the Oriental faunal region, relatively small in size, has not experienced much aridity except in India, where

Palearctic bees rather than derived Oriental ones have occupied the dry zones. The Oriental area does have a few distinctive subgenera or genera, restricted to or at least centered in the Oriental region. These include *Pachyhalictus*, *Hoplonomia*, certain small anthidiine taxa, subgenera of *Xylocopa* and *Ceratina*, *Thygatina*, *Elaphropoda*, *Protomelissa*, *Lepidotrigona*, and *Apis*.

The Oriental fauna is enriched by a few groups from Australia and a larger number from the Palearctic. Groups centered in Australia that have probably dispersed northwestward are *Homalictus* and *Austronomia*. Some of the primarily Palearctic taxa are the same taxa that enter Africa, but most invaded the tropics separately in Africa and in Asia. Groups involved include *Halictus* s. str. and *Seladonia*, *Sphecodes*, *Systropha*, *Andrena*, *Hoplitis*, *Nomada*, and *Bombus*.

The tropical part of the *Neotropical region* is characterized by the abundance of Meliponinae, including the genus *Melipona*. Disjunct distributions and poor dispersal abilities suggest that meliponines may have originated before the fragments of Gondwanaland became widely separated (see also Moure, 1951). The large group of genera of augochlorine halictids is also abundant in the tropics and must be ancient, considering its size and diversity. Its absence in Africa and Australia suggests that it postdates the breakup of Gondwanaland, as could be true for the Halictidae as a whole. Other largely tropical groups in the New World also lack close relatives elsewhere. These include various exomalopsine and nomadine genera, Tetrapediini, Centridini, Ctenioschelini, Euglossini, Rathymini, and certain subgenera of megachilids, xylocopines, etc. Some of these groups extend beyond the tropics both northward and southward, but all are to a major extent tropical. Some such taxa could have arisen from those that were in South America when it separated from Africa in Albian and Cenomanian times (Förster, 1978) (100 m.y. BP), but it is perhaps more likely that the ancestors of most of them arrived later and crossed the still narrow Atlantic, for there is no certainty that bees existed 100 m.y. BP, and the Atlantic remained narrow in the equatorial region for a long time.

The fact that meliponine distribution is best explained by assuming that these bees were in Gondwanaland before its break-up should be viewed with the understanding that it was the tropical parts of South America and Africa that separated last and were separated by narrow and probably island-filled seas. It would be more accurate to say that the Meliponinae were in Gondwanaland before its fragments became so isolated that the bees were unable to cross occasionally by rafting or other means. Presumably other bees would be more likely to cross such seas than Meliponinae. Lack of distributional evdience for such crossing by other groups of bees suggests that they were not yet present in the moist tropics when the continents separated.

There must also have been various taxa of bees that reached South America by island-hopping from North America during the Tertiary, evolved there, and became part of the Neotropical fauna. Any and perhaps all of the Neotropical groups listed above except the Meliponinae might fall in this category.

Several primarily Nearctic or Holarctic types extend in little modified condition into the Neotropics. Examples are *Halictus* (2 subgenera, *Halictus* s. str. to Trinidad and Colombia, *Seladonia* to central Brazil); *Calliopsis*, *Andrena*, and

Heriades (to Panama); *Anthophora* (to Argentina); and *Bombus* (to Tierra del Fuego). Such forms are far less numerous than the many Neotropical taxa that have a few species in the Sonoran or Chihuahuan deserts or other Nearctic areas. Thus in the recent interactions of the faunas, more tropical forms have adapted to seasonal warm north temperate areas than northern forms that have adapted to the tropics. The genera listed above probably entered South America since it was nearly or fully united with North America (union was about 5.7 m.y. BP).

The Neotropical bee fauna of North and Central America is much like that of tropical South America, although as indicated above, there is a small admixture of northern types such as *Andrena* and *Calliopsis*. Whatever tropical-adapted bees evolved in tropical North America and in Central America (insular or not) have become completely intermixed with those of South America, or belonged to the tropical South American groups to begin with, so that no distinction is now possible between tropical groups of South American and of North American origin.

Mountains, of course, have added greatly to the diversity of genera and species of the Neotropical fauna, but they are only part of the reason for the richness of this fauna compared to that of other tropical regions. Collecting experience and the meager data in Table 1 suggest that a given square mile of lowland forest contains many more species than an equivalent square mile in Africa or the Oriental region. A history of alternating wet and dry epochs (Haffer, 1969) with neither phase ever eliminating the other, may be responsible for this faunal richness. Likewise the much more extensive and diverse south temperate area, rich in bees, in South America than in Africa may have provided a source for tropical forms.

The *Antilles* contain only 18 tribal to familial taxa. *Nesomelecta* is considered distinct at the generic level and *Alayoapis* at the subgeneric level but otherwise all the forms are only specifically distinct from their continental relatives. Presumably, as for most other groups of organisms, the whole Antillean fauna must have arrived across the water. The fauna is depauperate Neotropical although there are a few taxa of Nearctic origin (*Nomia*, *Halictus*, *Heriades*). The greatest interest of the Antillean fauna from our standpoint is that it gives some idea of the island-hopping abilities of the various groups and of the faunas that must have inhabited the islands that existed in the seas between North and South America during much of the Tertiary, and that must have facilitated the faunal interchange between these continents.

The *southern Brazilian to Argentina region* has a large bee fauna. The southern part of the tropics in central and southern Brazil is progressively enriched as one goes southward by a mesic south temperate fauna, which also extends through Uruguay, and parts of Paraguay and Argentina. Group after group of Neotropical bees has additional genera or subgenera in this area. Thus this is the richest region, at least in the Neotropics, for Augochlorini, Panurginae, Exomalopsini, Nomadini, Eucerini, Xylocopini, etc. Since tropical forest fingers (e.g., along the coast, in the Paraná valley, and at Tucumán) extend into the savanna and grassland, many thoroughly tropical taxa also extend far south, with the result that the area of southern Brazil to Argentina has one of the richest mesic bee faunas in the world. Laroca's (1974) list is based on only three small areas (Table 1). To the south-

west the savanna and grassland part of southern Brazil–Argentina gradually becomes more xeric until in central Argentina there is desert vegetation similar in appearance to that of the Sonoran desert. Jörgensen's (1912) list of species of Mendoza shows something of the richness of this area.

The *Araucanian region* has a quite different bee fauna, lacking many of the typical Neotropical groups such as Meliponinae and Euglossinae, and having various unique and probably relict groups such as *Diphaglossa*, *Cadeguala*, *Corynura*, *Neofidelia*, *Manuelia*, and *Eucerinoda*. It is particularly rich in *Alloscirtetica* and Xeromelissinae, and has a larger diphaglossine fauna than any other area. It is also enriched by three genera which probably arrived by long distance dispersal from North America—*Penapis* (Dufoureinae), *Orphana* and *Euherbstia* (Andreninae).

Both temperate South American areas considered above share in an abundance of Paracolletini. Except for Australia, this is the only region where this group is abundant. The Araucanian region also contains *Neofidelia*, the only fideliid known outside of southern Africa. The Gondwanaland source of such bees seems clear.

The moderate to high-altitude fauna of the Andes is probably mostly derived recently (since elevation of the Andes in late Tertiary) from faunas of southern South America, perhaps primarily from the Araucanian. Thus it includes *Alloscirtetica* and Paracolletini. It also includes characteristic genera of Augochlorini (e.g., *Andinaugochlora*), presumably derived from the fauna of southern Brazil to Argentina, or possibly directly from that of the wet tropics.

The *Nearctic region* shares many taxa with the *Palearctic region*, and the two are quite legitimately joined to form the Holarctic. Certain genera (*Systropha*, *Rhophites*, *Panurgus*, *Dasypoda*, *Thyreus*, and others) are present in the Palearctic but absent in the Nearctic. At the tribal and subfamilial levels only some small taxa (Apinae, Nomioidini, Pararhophitini, and Ammobatoidini) are present in the Palearctic but not the Nearctic regions.

Dispersal across the North Pacific, and earlier in the Tertiary no doubt across the North Atlantic, is responsible for the similarity of the faunas of the two northern continents. To judge by the various Eurasian groups that reach North America only or chiefly in the west, most of the recent dispersal has been from Asia to North America and not in the reverse direction. Examples are *Chelostoma*, *Anthocopa*, *Dioxys*, *Melecta*, *Panurginus*, etc. Dispersal from North America to Eurasia, however, must have occurred, as illustrated by groups of Neotropical origin like *Nomada* and *Epeolus* that now range throughout the Holarctic area.

In contrast to the few Palearctic groups that do not reach the Nearctic region, there are many major taxa in the Nearctic region that do not reach the Palearctic. Nearly all have southern affinities. Some are clearly of Neotropical origin, such as *Caupolicana*, three genera of Augochlorini, *Protandrena*, various subgenera of *Megachile* and *Coelioxys*, *Exomalopsis* (2 subgenera), *Centris* (2 subgenera), one or more subgenera of *Nomada*, etc. Moreover, there are various groups found in both North and South America, more or less equally, which I believe to be of southern origin and which do not occur outside of the Western Hemisphere. Examples are Oxaeidae, *Agapostemon*, *Diadasia*, *Melitoma*, *Ancyloscelis*, and *Ptilo-*

thrix. Finally, a number of Neotropical taxa extend marginally into the Nearctic region, mostly in the Chihuahuan and Sonoran areas (for example, *Pseudaugochloropsis*, *Ptiloglossa*, *Temnosoma*, *Ptilomelissa*). The result is that the Nearctic region contains more tribes, subfamilies, and families of bees than the Palearctic or any other major faunal region (Table 3) and more genera and subgenera than any major fauna except the Neotropical.

The Palearctic fauna is also large and diverse (Table 3). Many groups are more abundant and diversified in the Palearctic region (including the Mediterranean) than elsewhere in the world. Examples are Bombini, *Halictus*, *Hoplitis*, Anthidiini, Dioxini, Anthophorini, and Melectini. A few predominantly African or Oriental groups appear to have remained in the southern Palearctic as the rest of the tropical fauna retreated with climatic deterioration, or extended north from Africa or the Orient into the southern Palearctic. Examples are *Nomia*, *Nomioides*, *Thrincohalictus*, *Exoneuridia*, *Ctenoplectra* (in the eastern Palearctic), *Amegilla*, *Thyreus*, and perhaps *Xylocopa* and *Ceratina*. Most of these forms probably arrived in the Palearctic in or since the Miocene when Africa and Eurasia were reunited. Except for *Exoneuridia* and *Thrincohalictus*, found only in Asia Minor, Palearctic species of all the genera listed are similar to African or Oriental species. Some groups probably entered the Palearctic from the Nearctic. Outstanding examples are the Exomalopsini-Ancylini, *Nomada*, and *Epeolus* (see section on DISJUNCTIONS), all of them ultimately Neotropical in origin.

The *Madrean area* (Californian plus the Sonoran and Chihuahuan deserts) is the climatic equivalent of the Mediterranean–Central Asiatic region, but appears to have had much better access to a tropical fauna than has the Old World equivalent. This applies especially to the Sonoran and Chihuahuan regions. In addition to the Nearctic taxa listed previously as originating in the Neotropics (*Caupolicana*, three genera of Augochlorini, etc.) and as widespread American (Oxaeidae, *Agapostemon*, etc.), all of which except *Augochlora* occur in the Madrean as well as the true Nearctic region, there are numerous Neotropical groups that occur in the Madrean, especially in the deserts, but do not or scarcely range into the mesic areas to the north of it. Such taxa are *Ptiloglossa*, *Zikanapis*, additional augochlorine genera, certain subgenera of *Centris*, Cteniochelini, and others. Most of the amphitropical genera listed in the section on DISJUNCTIONS are of south temperate origin and in the north are confined to or centered in the Madrean deserts. A noteworthy feature of the Nearctic region, and especially of the Madrean area, is the abundance of Panurginae, in sharp contrast to the Palearctic region.

The bee fauna of the Sonoran and Chihuahuan deserts may be roughly divided into two categories: first, those forms which have their seasonal flight in the spring and which collect pollen chiefly from the spring-flowering herbs, mostly annuals; and second, those forms which may or may not have their flight season in the spring and which collect pollen chiefly from typically Neotropical groups of plants, mostly trees and shrubs, that have penetrated the Sonoran region. Examples of such plants are *Larrea*, *Prosopis*, and *Cercidium*. The first group of bees consists of practically unmodified northern types (e.g., species of *Andrena*, *Anthophora*, *Synhalonia*, *Osmia*), the plants upon which they feed being likewise

northern and little modified except for shortening of the seasonal period of development as an adaptation to the xeric conditions. The second group of bees consists partly of southern types such as *Caupolicana*, *Protoxaea*, *Protepeolus*, *Martinapis*, *Centris*, and *Exomalopsis* (for details, see Michener, 1941), and partly of North American groups at least some of which are derived from northern groups of bees, e.g., *Ashmeadiella* and *Proteriades* derived from *Hoplitis* (= *Anthocopa*) and *Perdita*, a North American panurgine group of unknown derivation.

As in certain other xeric regions, there are in the Madrean area certain bees which appear to be relict forms. These include *Hesperapis*, *Megandrena*, and *Xeralictus*.

Although the arid part of the Palearctic region, i.e., the zone from the *Mediterranean basin to Central Asia* and beyond, contains an extremely rich fauna, it consists almost exclusively of the same tribal to familial groups that are in the mesic Palearctic. Some groups particularly richly represented in this xeric zone are Halictini, Anthidiini, osmiine Megachilini, Anthophorini, Dioxini, Melectini. Some groups largely limited to it are Ancylini, Pararhophitini, and *Eremaphanta*.

There are almost no taxa found in Africa and the Mediterranean basin but not also in more northern Eurasia, although such genera as *Nomia* and *Nomioides* nearly qualify as do certain Megachilinae. As indicated above in the account of the Palearctic, a few other genera that appear to be of southern origin extend well into the Palearctic region. Perhaps because the reservoir of tropical taxa is smaller in Africa than in the Neotropics, and because the major barriers (climatic, water, and montane) run east and west, the penetration of tropical types into the north temperate zone was much less in the Old World than in America.

Summary

The bees arose from sphecoid wasps, probably in the upper Cretaceous, and perhaps in the arid parts of West Gondwanaland (Africa, South America). The earliest fossils, however, are from the late Eocene of Europe and these fossils include derived long-tongued bees (Apidae) as well as short-tongued bees of presumably more primitive families. The principal evolutionary achievement of the ancestral bees was their transfer from animal food to complete dependence on angiosperm floral resources. Bees have been much less successful than the angiosperms in adapting to humid conditions, and are still most abundant and diversified in some of the warm temperate arid regions of the world, especially those of North America and Eurasia. By contrast, bees, unlike many groups of organisms, are not unusually numerous or diverse in the tropics. The oriental tropics have a particularly poor fauna (89 genera and subgenera). Africa has a larger fauna (although perhaps not in the wet tropics) which was perhaps enlarged during dry periods that appear to have exterminated many organisms of the wet tropics. There are 175 genera and subgenera in tropical and austral Africa. The Neotropics with 315 genera and subgenera are relatively rich in bees, even in the wet tropics, perhaps because there has been a fluctuating pattern of both forest and savanna, and also because of continuity of the tropical region with the rich warm temperate fauna of South America. The comparable south

temperate fauna of Africa occupies a limited area and for this reason could not have been as rich a source of bees for the tropics; for the oriental tropics there is no comparable south temperate source except Australia which is isolated by ocean.

The diversity of faunas of major areas of the earth can often be related to interchanges among such areas. For example, the Nearctic faunal region (260 genera and subgenera) is richer than the Palearctic (243 genera and subgenera) largely because of the Neotropical elements in the Nearctic fauna. The main barriers between the Palearctic and nearby tropics (the Mediterranean Sea, the Saharan and Arabian deserts, the Himalayas, etc.) appear to have been more effective than the primarily climatic barriers between tropical North and Central America and temperate North America. Indeed, the Neotropics (presumably South America) appears to be the area of origin of some major groups of bees that have dispersed probably by island hopping to North America and thence spread widely. The best examples are *Nomada* and *Epeolus*, parasitic genera which were probably able to disperse extensively because of common, widespread, and previously unexploited hosts.

The distribution of most groups of bees can be explained on the basis of continents in approximately their present positions, without recourse to long-distance dispersal or great continental movements. No doubt this reflects the relatively recent origin and spread of most groups of bees. That dispersal across moderate ocean barriers can occur, however, in spite of fixed nest site preferences, is shown by the bees of islands. Thus New Zealand bees are derived from Australian groups, etc. Small bees and bees nesting in stems or wood seem more likely to reach islands than moderate sized or large ground nesting bees. The bee faunas of the Antilles and of certain of the Indonesian islands indicate that many bees can cross moderate ocean barriers and may use intervening islands in crossing broader oceans. Thus there was probably considerable faunal interchange via island stepping stones between continents such as North and South America, even when these continents were not connected

While slow spread across continents and dispersal across currently moderate-sized barriers can account for most bee distributions, there are various, probably ancient groups for which distributional discontinuities can best be explained by continental movements or dispersal across oceans when they were relatively narrow. Examples are the paracolletines, almost entirely limited to temperate parts of the three southern continents, and the fideliids, limited to south and southwest Africa and Chile. The stingless honeybees (meliponines), limited to the tropics and southern subtropical regions, have several subgroups each occurring in two or three of the tropical land areas of the earth. Continental movements may well account for this distribution, especially since Africa and South America were connected or close together far longer in the equatorial region than in temperate areas.

The other disjunctions discussed are likely to be of much more recent origin. Certain amphitropical distributions almost certainly involve long distance dispersal, probably facilitated by dryer periods that reduced the distance between favorable habitats as compared to the present. Thus a considerable number of taxa of bees is found in warm temperate South America (mostly in deserts or

semi-deserts) and in the Sonoran and Chihuahuan deserts and sometimes elsewhere in North America, but not in the intervening tropics.

Another group of disjunctions involves the tropical and subtropical parts of Africa and the Orient. These areas could be nearly connected for bees living in grasslands or savanna by a somewhat moister climate across the Arabian peninsula, a likely condition at intervals in the past. Likewise, climatic change can account for various other disjunct distributions.

There remain several disjunctions for which no reasonably convincing explanation exists. All involve single taxa or groups, not groups of taxa, and therefore may result from isolated unlikely dispersal events. Given time, such unlikely events are likely to occur.

Many bees are restricted in pollen collecting to particular kinds of flowers. As one might expect, the distribution of such oligolectic bees is limited by the occurrence of host flowers. Some such bees have spread far beyond their original range when the plant has been dispersed by agriculture or horticulture. Most oligolectic bees, however, do not exist over the entire range of their floral host or do not occur with all populations of the host plant. It is clear that most plants, even when recognizable plant-bee coevolution has occurred, can exist and reproduce for long periods without their oligoleges, pollination from general pollinators such as polylectic bees sufficing. Indeed some oligoleges have nothing to do with pollination, but merely harvest pollen without transferring any to the stigmas, and thus are in effect parasitic.

The frequency of oligolecty appears to vary with climate, and is probably positively related to the number of kinds of bees simultaneously in flight in an area. Oligolecty is common, for example, in xeric North American areas, less common in mesic areas, and is rare in the tropics. Presumably it reduces competition among species, and would be especially important in areas like deserts with brief flowering seasons and many kinds of bees.

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THE GENUS *BOUTELOUA* (POACEAE)[1]

FRANK W. GOULD[2]

ABSTRACT

Bouteloua was established in 1805 by Mariano Lagasca. The type species is *B. curtipendula* (Michaux) Torrey, originally named *B. racemosa* by Lagasca. In the present treatment, 39 species are recognized, 29 of these restricted to North America and Central America, 2 species are endemic to the Antilles, 2 species occur in the Antilles, as well as at other locations, 5 species are distributed in both North and South America, and 1 species, *B. megapotamica*, is represented only in southern South America. *Bouteloua* is a characteristic member of the tribe Chlorideae of the subfamily Eragrostoideae (Chloridoideae). The species all are C_4 plants with typical Kranz leaf anatomy and starch storage features. Chromosome numbers have been reported for 29 species with most species being diploid ($2n = 20$) or tetraploid ($2n = 40$). Aneuploid records or series of counts have been reported for 9 species.

Bouteloua has long been recognized as one of the important grass genera of the central and southern North American prairies and plains. Not only do species of the genus comprise significant elements of many grassland formations but a number are among the most valuable forage species of the southern and southwestern grazing areas. Perhaps most widespread and economically important of the 39 recognized species are *B. curtipendula*, sideoats grama, *B. gracilis*, blue grama, *B. eriopoda*, black grama, and *B. hirsuta*, hairy grama.

The genus *Bouteloua* is restricted in its natural distribution to the New World. Thirty-four species are distributed in North and Central America, and islands of the West Indies and the Caribbean. Five species, *B. americana*, *B. curtipendula*, *B. disticha*, *B. media*, and *B. repens*, are present both in North and South America and one species, *B. megapotamica*, has a restricted range in South America. The widespread and polymorphic *B. curtipendula* has been introduced into the Hawaiian Islands and elsewhere as a potential forage grass.

Most comprehensive of the numerous publications concerning the taxonomy of *Bouteloua* is that of David Griffiths (1912) entitled, *The Grama Grasses: Bouteloua* and *Related Genera*. Hitchcock (1920, 1935) and Hitchcock et al. (1939) contributed significantly to our knowledge of the North American species. The present treatment is based largely on investigations of the writer and his associates, presented in the following publications: Gould, 1949, 1951, 1958, 1959, 1960, 1963, 1964, 1965, 1966, 1968a, 1968b, 1968c, 1969, 1975, 1976; Gould & Kapadia, 1962a, 1962b, 1962c, 1964; Gould & Soderstrom, 1970; Kapadia & Gould, 1964a, 1964b; Mohamed & Gould, 1966; Roy & Gould, 1971. Most of the *Bouteloua* research was conducted as Project S-1516 of the Texas Agricultural Experiment Station, with grant support from the National Science Foundation (grants G6372, G19438, continuation GB-120, GB-2491, and B7-1839R). The intent of the author in the present treatment is to consolidate and condense the information now available concerning

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Bouteloua taxonomy. The writer is deeply indebted to Robert B. Shaw for the fine distribution maps which have been prepared for all recognized *Bouteloua* taxa.

All species of *Bouteloua* are characterized by features of the Kranz Syndrome. They are C_4 in their photosynthesis and have the characteristic chloridoid leaf anatomy. Starch storage is in specialized plastids of the leaf sheath bundles, and the arrangement of cells in the leaf blade is typically Kranz. The 39 recognized species all are variously adapted to shortgrass prairies, desert grasslands, and xeric sites along desert shrub areas, and sandy shores.

Gross Morphology

Bouteloua is a genus of tufted annuals and perennials with spikelets closely placed and sessile on short, unbranched spicate primary branches of a slender panicle. The branches are solitary at the nodes. In the typical subgenus the branches are numerous and few-flowered whereas in subgenus *Chondrosium* the branches are few but bear numerous spikelets. In *B. simplex* and *B. scorpioides* there is a single terminal or subterminal branch and in other species the branches frequently or occasionally are reduced to one. Spikelets of *Bouteloua* have a single perfect floret below and 1–3 staminate or neuter, often rudimentary, florets above. A more complete description of the *Bouteloua* plant habit is presented in the taxonomic description of the genus.

Anatomy

STEM ANATOMY

In all species examined the culm internode is "solid," with ground tissue of large, thin-walled cells occupying the central area (Metcalfe, 1960; Gould, 1968c). Vascular bundles are restricted to the cortical zone or present in the cortex and in two or three rings in the outer half of the ground tissue.

LEAF ANATOMY

As viewed in tranverse section, the *Bouteloua* leaf blade is characteristically chloridoid. Vascular bundles with a single bundle sheath of large cells are separated by narrow bands of small, tightly packed, radially arranged chlorenchyma cells. In *B. pectinata* the vascular bundles and the associated bands of chlorenchyma of the central three-fourths or so of the blades are separated by bands of colorless cells which are continuous with the bulliform cells of one or both epidermises (Roy, 1968; Gould, 1968c). The colorless cells are absent from the lateral portions of the blade.

EPIDERMIS

In the species of *Bouteloua* examined, the short-cells were mostly in rows of 3–5 or more and usually present only in the costal zones. Silica bodies of the short-cells are reported to be saddle-shaped in *B. curtipendula*, *B. hirsuta*, and *B. pectinata*. The bicellular microhairs are clavate in all species reported, with the

distal cell having relatively thinner walls than the basal cell. Subsidiary cells of the stomata are reported to be triangular.

EMBRYO

Reeder (1957) reported the embryos of six species of *Bouteloua* to be of the eragrostoid-chloridoid type, with the vascular traces to the scutellum and plumule diverging separately, the epiblast present, the lower portion of the scutellum separated by a cleft from the coleorhiza, and embryonic leaves with overlapping margins. Also, as is characteristic of eragrostoid-chloridoid (and panicoid) grasses, the embryos is relatively large in respect to the size of the grain, usually being 40–90% the length of the endosperm.

CYTOLOGY

Chromosome numbers have been reported for 29 species of *Bouteloua*. The mass of evidence obtained indicates a single basic number of $x = 10$ for the genus. Early records of $2n = 28$, 35, and 42 by Fults (1942) were interpreted as indicating a basic number of $x = 7$. The counts of Fults may or may not have been accurate but no additional evidence has been brought forward to support the contention of a basic number of $x = 7$.

Chromosome records for *Bouteloua* taxa are presented in Table 1. Counts which I deem questionable or incorrect are in parenthesis. Published records for the 29 species of *Bouteloua* that have been cytologically investigated indicate that 11 are diploids, 7 tetraploids, 1 hexaploid, 8 have two levels of ploidy, and 3 have 3 levels of ploidy. Aneuploids have been reported for 9 taxa, all of which also had euploid counts, except *B. curtipendula* var. *caespitosa* with chromosome numbers from $2n = 58$–103.

Of the 10 species of *Bouteloua* judged to be "the most widespread and frequent," only one (*B. eriopoda*) is diploid, two (*B. aristidoides*, *B. americana*) are tetraploid, four (*B. simplex*, *B. curtipendula*, *B. chondrosioides*, *B. barbata*) have two levels of ploidy, and three (*B. gracilis*, *B. hirsuta*, *B. repens*) have three levels of ploidy.

The lone diploid species of the "widespread and frequent" group, *B. eriopoda*, originally included a hexaploid population which was only recently elevated to specific status as *B. eriostachya*. *Bouteloua curtipendula*, with one diploid-tetraploid-aneuploid series of populations (var. *tenuis*), one diploid-aneuploid series (var. *curtipendula*), and one totally aneuploid series var. *caespitosa*), comprises the most complex and variable series of populations included in a single species. Also of note is *B. repens* with three levels of ploidy and nine recognizably different "forms" to which eight binomials have been applied but which cannot be satisfactorily segregated into specific or varietal entities.

No chromosome records have been reported for 10 species, *B. annua*, *B. distans*, *B. eludens*, *B. johnstonii*, *B. juncea*, *B. kayi*, *B. megapotamica*, *B. parryi*, *B. pedicellata*, and *B. vaneedenii*. Pollen grain measurements for *B. pedicellata*, *B. reflexa*, *B. vaneedenii*, and *B. disticha* indicate strongly that these species are diploid,

TABLE 1. Chromosome numbers in *Bouteloua*. (Counts in parenthesis are probably erroneus.)

Taxon	2*n*	Location	Reference
B. alamosana	40	MEXICO. Chiapas, Oaxaca	Gould, 1969, as *B. longiseta*
	60	HONDURAS. Morazán	Davidse & Pohl, 1972
B. americana	40	COSTA RICA. Puntarenas	Pohl & Davidse, 1971
	40	VENEZUELA. Guárico	Davidse & Pohl, 1974
B. aristidoides	40	TEXAS. Llano Co.	Gould, 1960
		MEXICO. Chihuahua, Durango	Reeder, 1971
B. barbata			
var. *barbata*	20	NEW MEXICO. Harding Co.	Reeder, 1977
	20	MEXICO. San Luis Potosí	Gould, 1965
	20	MEXICO. Baja Calif. Sur, San Luis Potosí	Gould, 1966
	20	MEXICO. Chihuahua	Reeder, 1971
	40	TEXAS. Hall Co.	Gould, 1958
	40	MEXICO. Coahuila	Gould, 1966
B. barbata			
var. *rothrockii*	20	ARIZONA. Pima Co.	Gould, 1976, as *B. rothrockii*
	22	ARIZONA. Pima Co.	Fults, 1942, as *B. rothrockii*
	40	ARIZONA. Cochise Co.	Reeder, 1977, as *B. rothrockii*
	40	ARIZONA. Pinal Co.	Gould, 1964, as *B. rothrockii*
	41	ARIZONA. Cochise Co.	Gould, 1976, as *B. rothrockii*
	42, 49	ARIZONA. Santa Cruz Co.	Gould, 1976, as *B. rothrockii*
	45, 47, 50	ARIZONA. Pinal Co.	Gould, 1976, as *B. rothrockii*
B. breviseta	(21)	Without locality	Fults, 1942
	(28)	TEXAS. Without locality	Brown, 1950
	40	TEXAS. Brewster Co.	Reeder, 1977
	40	TEXAS. Presidio Co.	Gould, 1964
	40	MEXICO. Coahuila	Gould, 1965
	40	MEXICO. Coahuila	Reeder, 1966
B. chasei	40	MEXICO. San Luis Potosí	Gould, 1965
	40	MEXICO. Nuevo León, San Luis Potosí, Zacatecas	Reeder, 1967
	40	MEXICO. San Luis Potosí	Reeder, 1968
	40	MEXICO. Nuevo León	Reeder, 1971
	40	MEXICO. Nuevo León	Reeder, 1966
B. chondrosioides	(14)	TEXAS. Without locality	Brown, 1940
	20	TEXAS. Jeff Davis Co.	Freter & Brown, 1955
	20	MEXICO. Aguascalientes, Jalisco	Reeder & Reeder, 1966
	20	TEXAS. Brewster Co.	Reeder, 1967
	20	MEXICO. Aguascalientes	Reeder, 1967
	20	MEXICO. Aguascalientes	Reeder, 1971
	22	MEXICO. Chihuahua	Gould, 1966
	40	ARIZONA. Pima Co., Santa Cruz Co.	Reeder, 1977
	40	MEXICO. Durango	Gould, 1958
	40	MEXICO. Oaxaca	Gould, 1965
	40	MEXICO. Chiapas	Gould, 1966
	40	MEXICO. Durango, Oaxaca	Reeder, 1967
	40	MEXICO. Chihuahua	Reeder, 1968
	40	MEXICO. Durango, Zacatecas	Reeder, 1971
B. curtipendula			
var. *curtipendula*	20	SOUTH DAKOTA. Haskon Co.	Reeder, 1977
	40	NEBRASKA, IOWA, OKLAHOMA	Fults, 1942
	40	OKLAHOMA, KANSAS, TEXAS	Gould & Kapadia, 1962a
	40	WYOMING. Crook Co.	Reeder, 1977
	41–44	COLORADO, ILLINOIS, KANSAS, OKLAHOMA, TEXAS	Gould & Kapadia, 1962a, var. *caespitosa* in part
	40–96	TEXAS	Freter & Brown, 1955
	42	Without specific locality	Nielsen & Humphrey, 1937
	(42)	COLORADO, KANSAS, IOWA, NEBRASKA, NEW MEXICO, NORTH DAKOTA, OKLAHOMA, TEXAS	Fults, 1942
	45	OKLAHOMA. Grady Co.	Fults, 1942
	45–64	TEXAS. Numerous locations in the central portion of the state	Gould & Kapadia, 1962a

TABLE 1. *Continued.*

Taxon	2*n*	Location	Reference
B. curtipendula var. *curtipendula* (continued)	56	TEXAS. Bell Co.	Fults, 1942
B. curtipendula var. *caespitosa*	58–103	ARIZONA. Pima Co., Santa Cruz Co. NEW MEXICO. Lima Co. TEXAS. Edwards Co., Jeff Davis Co., Kerr Co., Llano Co., Medina Co., Parker Co., Presidio Co., Shackelford Co., Stephens Co., Terrell Co., Uvalde Co., Val Verde Co. MEXICO. Chihuahua, Coahuila, Dist. Federal, Durango, Hidalgo, Puebla, Querétaro	Gould & Kapadia, 1964
	70	ARIZONA, TEXAS	Fults, 1942
	92	MEXICO. San Luis Potosí	Reeder, 1971
	98	COLORADO. Kiowa Co.	Fults, 1942
B. curtipendula var. *tenuis*	20	MEXICO. Durango, San Luis Potosí, Zacatecas	Gould & Kapadia, 1964
	20	MEXICO. Durango	Gould, 1958, as *B. curtipendula*
	40–41	MEXICO. Chiapas	Gould & Soderstrom, 1970
	40–42	MEXICO. Aguascalientes, Chihuahua, Durango, Jalisco, Zacatecas	Gould & Kapadia, 1964
B. disticha	40	COSTA RICA. Guanacaste, Puntarenas	Pohl & Davidse, 1971
B. elata	20	MEXICO. Chiapas	Gould, 1966
	20	MEXICO. Jalisco	Reeder, 1967
B. eriopoda	20	ARIZONA. Coconino Co.	Reeder, 1977
	20	ARIZONA. NEW MEXICO	Streetman & Wright, 1960
	20	TEXAS. Martin Co.	Reeder, 1967
	20	TEXAS. Culberson Co.	Gould, 1968a
	20	ARIZONA. Pima Co.	Streetman & Wright, 1960
	(21)	ARIZONA. Pima Co. NEW MEXICO. Dona Ana Co., Valencia Co.	Fults, 1942
	(28)	TEXAS. Without locality	Brown, 1950
B. eriostachya	60	MEXICO. Coahuila	Reeder, 1967
B. gracilis	20	WYOMING. Platte Co.	Reeder, 1977
	20	NEW MEXICO. 23 localities in the southeastern part of the state. TEXAS. 13 localities in the western part of the state	Snyder & Harlan, 1953
	20	MEXICO. Durango, México, Querétaro	Gould, 1965
	20	MEXICO. San Luis Potosí	Gould, 1966
	(21)	COLORADO	Fults, 1942
	(28)	ARIZONA, COLORADO, KANSAS, NEBRASKA, NORTH DAKOTA, NEW MEXICO	Fults, 1942
	(35)	COLORADO, IOWA, NEBRASKA, NEW MEXICO, NORTH DAKOTA, TEXAS, WYOMING	Fults, 1942
	40	Without specific location	Avdulov, 1931, as *B. oligostachya*
	40	NEW MEXICO. 42 localities in the eastern part of the state. TEXAS. 14 localities in the western part of the state	Snyder & Harlan, 1953
	40	MEXICO. Chihuahua, Hidalgo, México, San Luis Potosí	Gould, 1965
	40	TEXAS. Deaf Smith Co., Jack Co., Jeff Davis Co., Lamb Co., Randall Co., Swisher Co.	Gould, 1968
	42	Without specific locality	Nielsen & Humphrey, 1937
	(42)	ALBERTA, ARIZONA, COLORADO, IOWA, KANSAS, MONTANA, NEBRASKA, NEW MEXICO, NORTH DAKOTA, OKLAHOMA, TEXAS, WYOMING	Fults, 1942
	42	NEW MEXICO. 4 localities in the southwestern part of the state. TEXAS. 2 localities in the northwestern part of the state	Snyder & Harlan, 1953

TABLE 1. *Continued.*

Taxon	2*n*	Location	Reference
B. gracilis (continued)	60	NEW MEXICO. 11 localities in the east-central part of the state	Snyder & Harlan, 1953
	60	MEXICO. Veracruz	Gould, 1965
	60	TEXAS. Archer Co.	Gould, 1968
	61, 77	OKLAHOMA. Garfield Co., Payne Co.	Fults, 1942
	84	OKLAHOMA. (Fort Supply)	Snyder & Harlan, 1953
B. hirsuta	(12)	Location not specified	Whaley, 1955
	20	TEXAS. Coryell Co., Llano Co.	Gould, 1958
	20	TEXAS. Edwards Co.	Gould, 1968a
	20	TEXAS. Bosque Co., Mason Co., San Patricio Co., Young Co.	Roy, 1968
	21	TEXAS. Jim Hogg Co. (or Denton?)	Fults, 1942
	22	TEXAS. Kerr Co.	Gould, 1968a
	22	COLORADO. Washington Co. TEXAS. Coryell Co., Mason Co.	Roy, 1968
	24	MEXICO. México	Gould, 1965
	24	COLORADO. Kiowa Co. TEXAS. Burnet Co., Coryell Co., Sutton Co., Travis Co., Young Co.	Roy, 1968
	26	TEXAS. Burnet Co., Coryell Co., Gillespie Co.	Roy, 1968
	28	TEXAS. Without locality	Brown, 1951
	28	MEXICO. Hidalgo	Gould, 1965
	28	TEXAS. Jeff Davis Co., Menard Co.	Gould, 1968a
	28	TEXAS. Comanche Co., Lampasas Co., Travis Co.	Roy, 1968
	30	TEXAS. Bosque Co.	Roy, 1968
	32	COLORADO. Baca Co., Washington Co. TEXAS. Lampasas Co., Travis Co.	Roy, 1968
	34	NEW MEXICO. Dona Ana Co. TEXAS. Brazos Co., Montague Co.	Roy, 1968
	36	TEXAS. Burnet Co., Comanche Co., Llano Co., Montague Co.	Roy, 1968
	37	KANSAS. Ellis Co.	Fults, 1942
	40	MEXICO. Jalisco	Gould, 1965
	40	TEXAS. Williamson Co.	Gould, 1968a
	40	NEW MEXICO. Dona Ana Co. TEXAS. Brazos Co., Burnet Co., Montague Co., Young Co.	Roy, 1968
	42	OKLAHOMA. Payne Co.	Fults, 1942
	42	TEXAS. Brazos Co.	Gould, 1968a
	42	OKLAHOMA. Payne Co. TEXAS. Brazos Co., Brown Co., Lampasas Co., Montague Co., Nolen Co., Travis Co.	Roy, 1968
	43	TEXAS. Brazos Co., Comanche Co., Montague Co.	Roy, 1968
	44	TEXAS. Brazos Co., Gillespie Co., Mills Co., Montague Co.	Roy, 1968
	45	TEXAS. Travis Co.	Roy, 1968
	46	MEXICO. Durango	Gould, 1958
	46	MEXICO. Querétaro	Gould, 1965
	46	TEXAS. Crockett Co.	Gould, 1968a
	46	TEXAS. Blanco Co., Brazos Co., Burnet Co., Kendall Co., Montague Co., Travis Co.	Roy, 1968
	48	TEXAS. Brazos Co., Burnet Co., Lampasis Co., Travis Co.	Roy, 1968
	50	TEXAS. Blanco Co., Brown Co., Burnet Co., Travis Co.	Roy, 1968
	52	MEXICO. Jalisco	Gould, 1965
	52	TEXAS. Brazos Co., Burnet Co., Mills Co., Montague Co., Travis Co.	Roy, 1968
	53	TEXAS. Blanco Co.	Roy, 1968

TABLE 1. *Continued.*

Taxon	2n	Location	Reference
B. hirsuta (continued)	54	TEXAS. Kendall Co.	Roy, 1968
	56	TEXAS. Brazos Co., Gillespie Co., Travis Co.	Roy, 1968
	58	TEXAS. Mills Co.	Roy, 1968
	60	NEW MEXICO. Dona Ana Co. TEXAS. Brazos Co.	Roy, 1968
B. karwinskii	20	MEXICO. Zacatecas	Reeder, 1966
	20	MEXICO. Zacatecas	Reeder, 1967
	20	MEXICO. San Luis Potosí	Reeder, 1968
B. media	20	MEXICO. Guerrero, Morelos	Gould & Kapadia, 1964
	20	MEXICO. Chiapas, Oaxaca	Gould, 1966
	20	MEXICO. Chiapas	Gould & Soderstrom, 1970
	27	COSTA RICA. Guanacaste	Pohl & Davidse, 1971
B. pectinata	20	TEXAS. Without locality	Whaley, 1955
	20	TEXAS. Parker Co.	Gould, 1968a
	20	TEXAS. Blanco Co., Bosque Co., Burnet Co., Coryell Co., Erath Co., Gillespie Co., Hamilton Co., Hays Co., Kendall Co., Kerr Co., Lampasas Co., Parker Co., Travis Co., Wise Co.	Roy, 1968
B. purpurea	40	MEXICO. Guanajuato, México	Gould & Kapadia, 1964
	40	MEXICO. Querétaro	Gould, 1966
B. radicosa	20	Locality not reported	Freter & Brown, 1955
	60	MEXICO. Guanajuato, Jalisco	Gould, 1965
B. reflexa	20	MEXICO. Baja California Sur	Gould, 1966
B. repens	(14)	TEXAS. Without locality	Brown, 1950, as *B. filiformis*
	20	PUERTO RICO	Snyder & Harlan, 1953, as *B. heterostega*
	20	MEXICO. Guanajuato, Guerrero, Hidalgo, México, Puebla, Querétaro, San Luis Potosí	Gould, 1965, as *B. filiformis*
	20	ARIZONA. Pima Co., Santa Cruz Co. TEXAS. Hidalgo Co., Kleberg Co., Webb Co. MEXICO. Campeche, Guanajuato, Hidalgo, Mexico, Nuevo León, Querétaro, San Luis Potosí, Sonora, Tamaulipas, Veracruz, Yucatán	Gould, 1969
	20	MEXICO. Yucatán	Gould & Soderstrom, 1970
	20–22	ARIZONA. "central Arizona"	Snyder & Harlan, 1953, as *B. filiformis*
	21	MEXICO. Aguascalientes, Nuevo León, Querétaro, San Luis Potosí, Sonora	Gould, 1969
	22	MEXICO. Querétaro	Gould, 1965, as *B. filiformis*
	22	MEXICO. Nuevo León, Sonora, Querétaro	Gould, 1969
	23	MEXICO. Nuevo León, San Luis Potosí, Sonora	Gould, 1969
	40	MEXICO. Durango, Guerrero, Jalisco, Morelos, Oaxaca, Puebla, Tamaulipas	Gould, 1965, as *B. filiformis*
	40	ARIZONA. MEXICO. Chiapas, Durango, Guerrero, Morelos, Nuevo León, Oaxaca, Puebla	Gould, 1969
	ca. 40	DOMINICAN REPUBLIC. Santiago	Gould & Soderstrom, 1967, as *B. heterostega*
	ca. 45	MEXICO. Jalisco	Gould, 1965, as *B. filiformis*
	46	MEXICO. Guerrero	Tateoka, 1962, as *B. filiformis*
	60	MEXICO. Guerrero	Gould, 1965, as *B. filiformis*
	60	MEXICO. Baja California Sur, Guanajuato, Jalisco, Michoacán, Morelos	Gould, 1969
	60	HONDURAS, Morazán	Davidse & Pohl, 1972
B. rigidiseta	(28)	TEXAS. Without locality	Brown, 1950
	(35)	TEXAS. Denton Co.	Fults, 1942
	40	TEXAS. Brazos Co., Llano Co.	Gould, 1958
	40	TEXAS. Kimble Co.	Gould, 1968a
B. scorpioides	20	MEXICO. Nuevo León	Reeder, 1966

TABLE 1. *Continued.*

Taxon	2*n*	Location	Reference
B. scorpioides (continued)	20	MEXICO. Durango, Nuevo León, San Luis Potosí, Zacatecas	Reeder, 1967
	40	MEXICO. San Luis Potosí	Reeder, 1968
B. simplex	20	MEXICO. Nuevo León	Gould, 1965
	40	ARGENTINA. Las Huas	Covas, 1945
	40	MEXICO. Durango	Gould, 1960
	40	MEXICO. Hidalgo	Gould, 1965
B. triaena	20	MEXICO. México	Tateoka, 1962
	20	MEXICO. México, Oaxaca, Puebla	Gould & Kapadia, 1964
	20	MEXICO. Chiapas	Gould & Soderstrom, 1970
B. trifida	20	TEXAS. Jim Wells Co., Llano Co.	Gould, 1960
	20	MEXICO. Nuevo León	Gould, 1965
	20	MEXICO. Coahuila	Gould, 1966
	20	TEXAS. Frio Co., Kimble Co., Maverick Co., Val Verde Co.	Gould, 1968a
	20	MEXICO. Coahuila	Reeder, 1971
	(28)	TEXAS. Without locality	Brown, 1950
B. uniflora var. *uniflora*	20	TEXAS. Edwards Co., Kendall Co., Kerr Co., Sutton Co.	Freter & Brown, 1955
	20	Locality not specified	Whaley, 1955
	20	TEXAS. Kerr Co., Kimble Co., Terrell Co., Tom Greene Co.	Gould & Kapadia, 1964
B. uniflora var. *coahuilensis*	20	MEXICO. Coahuila	Gould & Kapadia, 1964
B. uniflora var. *uniflora* hybrid	30	TEXAS. Terrell Co.	Gould & Kapadia, 1964, the plant a presumed *B. uniflora* × *B. curtipendula* hybrid
B. warnockii	21	NEW MEXICO. Dona Ana Co.	Gould & Kapadia, 1964
	22	TEXAS. Culberson Co.	Gould & Kapadia, 1962b
	23	NEW MEXICO. Dona Ana Co.	Gould & Kapadia, 1964
	25	TEXAS. Culberson Co.	Gould & Kapadia, 1962b
	25	NEW MEXICO. Dona Ana Co.	Gould & Kapadia, 1964
	28	TEXAS. Culberson Co.	Gould & Kapadia, 1964
	38	TEXAS. Culberson Co.	Gould & Kapadia, 1964
	40	TEXAS. Culberson Co.	Gould & Kapadia, 1964
B. williamsii	20	MEXICO. Jalisco, Oaxaca, Zacatecas	Gould, 1969
	20	MEXICO. Jalisco, Zacatecas	Reeder, 1971
	20	MEXICO. Oaxaca	Davidse & Pohl, 1978

with $2n = 20$ (Kapadia & Gould, 1964a). All of the taxa for which specific chromosome counts have not been reported have limited distributions and could be classified as rare or infrequent.

GENERIC RELATIONSHIPS

Bouteloua is a characteristic member of the tribe Chlorideae. The genus lies close to *Chloris* from which it differs most significantly in having the inflorescence branches borne singly and alternately arranged along the culm axis rather than digitately or verticilled. In several species of *Bouteloua* the branches are regularly or occasionally solitary and in a few species now grouped in *Chloris* (Anderson, 1974) the branches are irregularly clustered or clumped. The spikelets of *Bouteloua* and *Chloris* are similar, and in both there is a simple perfect floret below and one to few reduced florets above. Also close to *Bouteloua* are the mono-

typic, dioecious Mexican genera *Buchlomimus* Reeder, Reeder & Rzedowski and *Cyclostachya* J. & C. Reeder. These taxa were treated as species of *Bouteloua* in *North American Flora* (Hitchcock et al., 1939). Gould (1968b) described the monotypic genus *Neobouteloua*, based on the South American taxon long recognized as *Bouteloua lophostachya* Grisebach. *Neobouteloua* is readily distinguished from *Bouteloua* on the basis of its inflorescence with scattered and irregularly disposed branches.

Included with *Bouteloua* in Griffiths's 1912 treatment of the grama grasses were the genera *Triaena* H.B.K., *Pentarrhaphis* H.B.K., and *Cathestecum* Presl. The single species of *Triaena*, *T. racemosa* H.B.K. is inseparable from *Bouteloua* and is herein recognized as *B. triaena* (Trinius) Scribner. The small, New World genus *Pentarrhaphis*, with three tropical-subtropical species, appears very close to grasses of *Bouteloua* subgen. *Bouteloua*. In *Pentarrhaphis* the spikelets are 2-flowered, and the readily deciduous inflorescence branches bear 2 spikelets. *Cathestecum*, a somewhat larger New World genus centered in Mexico, has 2–3-flowered spikelets borne in clusters of 3 on readily deciduous branches. Characteristically the lateral (lower) spikelets of the cluster are staminate or sterile and only the lower floret of the terminal spikelet is pistillate.

SYSTEMATIC TREATMENT. Taxonomic History. The genus *Bouteloua*[3] was described in 1805 by Mariano Lagasca. Lagasca proposed five species, *B. racemosa*, *B. hirsuta*, *B. barbata*, *B. simplex*, and *B. prostrata*, but did not designate a type species. Griffiths (1912), Hitchcock (1920), and Hitchcock et al. (1939) all have accepted the first species, *B. racemosa*, as the type. As plants of the type species had been named *Chloris curtipendula* by Michaux in 1803, the legitimate name for this taxon is *Bouteloua curtipendula*.

Between 1806 and 1846, 11 generic names were proposed for various species and species groups of *Bouteloua*.

Atheropogon Muhl. in Willd., Sp. Pl. 4: 937. 1806. Based on *A. apludioides* Muhl., the type from temperate North America. This is *Bouteloua curtipendula* (Michaux) Torrey.

Triathera Desvaux, Nouv. Bull. Sci. Soc. Philom. Paris 2: 188. 1810. Based on *Aristida americana* L., the type from the Antilles. This is *Bouteloua americana* (L.) Scribner.

Heterosteca Desvaux, Nouv. Bull. Sci. Soc. Philom. Paris 2: 188. 1810. Based on *Heterosteca juncifolia* Desvaux, the type from the Antilles. This is *Bouteloua repens* (H.B.K.) Scribner & Merrill, not *B. juncifolia* Lag. or *Triathera juncea* Desvaux ex Beauvois [*Bouteloua juncea* (Desvaux ex Beauvois) Hitchcock].

Chondrosium Desvaux, Nouv. Bull. Sci. Soc. Philom. Paris 2: 188. 1810. Based on *Chloris procumbens* Durand, the type from Peru. This is *Bouteloua simplex* Lag.

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[3] Named in honor of two Spanish gardeners, the Boutelou brothers. Lagasca's original spelling of the genus name was *Botelua*. In a later publication (1816), he corrected this to *Bouteloua*.

Actinochloa Willd. ex Beauvois, Ess. Agrost. 41. 1812. Based on *Chondrosium procumbens* (Durand) Desvaux. This is *Bouteloua simplex* Lag.

Dineba Beauvois, Ess. Agrost. 98. 1812. Probably based on *Aristida americana* L. This is *Bouteloua americana* (L.) Scribner.

Polydon H.B.K., Nov. Gen. Sp. Pl. 1: 174. 1816. Based on *P. distichum* H.B.K., the type from Ecuador. This is *Bouteloua disticha* (H.B.K.) Bentham.

Triaena H.B.K., Nov. Gen. Sp. Pl. 1: 178. 1816. Based on *T. racemosa* H.B.K., the type from Mexico. This is *Bouteloua triaena* (Trinius) Scribner, not *Bouteloua racemosa* Lag.

Eutriana Trinius, Fund. Agrost. 161. 1820. Trinius listed two species, *E. curtipendula* and *E. bromoides*. The first, accepted as the type by Hitchcock (1920), is based on *Chloris curtipendula* Michaux (type from southern Illinois). This is *Bouteloua curtipendula* (Michaux) Torrey.

Aristidium (Endl.) Lindley, Veg. Kingdom 116. 1846. This is *Eutriana* Trinius section *Aristidium* Endl., based on *Dineba aristidoides* H.B.K., the type from Mexico. This is *Bouteloua aristidoides* (H.B.K.) Grisebach.

Triplathera (Endl.) Lindley, Veg. Kingdom 116. 1846. This is *Eutriana* Trinius section *Triplathera* Endl., based on *Eutriana multiseta* Nees, the type from Uruguay. This is *Bouteloua megapotamica* (Sprengel) Kuntze.

BOUTELOUA Lag.

Low, tufted *annuals* and caespitose or sod-forming *perennials*, some with stolons or rhizomes. *Leaves* mostly basal, with rounded sheaths and linear, flat or folded blades. *Ligule* commonly a ring of hairs. *Infloresecence* with 1 to numerous short, spicate branches; branches solitary at the nodes, closely or distantly spaced along the slender, erect main axis, with 1 to numerous sessile spikelets closely or loosely spaced in 2 rows along the margins of an angular of flattened rachis. *Disarticulation* at the base of the branch rachis or above the glumes. *Spikelets* with 1 perfect floret and 1–3 staminate or sterile (often rudimentary) florets above. *Glumes* shorter to longer than the perfect floret, unequal to nearly equal, 1-nerved, awnless or short-awned. *Lemma of the lower floret* 3-nerved, awnless or more frequently the midnerve and often the lateral nerves extending into an awn. *Palea* membranous, the 2 nerves occasionally awn-tipped.

The species of *Bouteloua* comprise two well-defined subgenera, these differing in several characters of the inflorescence and spikelets. Perhaps most consistent of the differences is the deciduous nature of the inflorescence branch in subgen. *Bouteloua*. No intergradation between the subgenera is apparent although divergence within each of the groups has resulted in a slight overlap of characteristics in a few taxa.

Bouteloua Lag. subgen. **Bouteloua**

Bouteloua Lag., Varied. Ci. 2(4): 134. 1805.
Atheropogon Muhl. in Willd., Sp. Pl. 4: 937. 1806.
Triathera Desvaux, Nouv. Bull. Sci. Soc. Philom. Paris 2: 188. 1810.
Heterosteca Desvaux, Nouv. Bull. Sci. Soc. Philom. Paris 2: 188. 1810.
Actinochloa Willd. ex Beauvois, Ess. Agrost. 41. 1812.

Dineba Beauvois, Ess. Agrost. 98. 1812.
Polydon H.B.K., Nov. Gen. Sp. Pl. 1: 174, *pl.* 55. 1816.
Triaena H.B.K., Nov. Gen. Sp. Pl. 1: 178. 1816.
Eutriana Trinius, Fund. Agrost. 161. 1820.

Inflorescence branches characteristically 7–80, mostly 0.8–2 cm long including the spikelets. *Disarticulation* at the base of the branch rachis. *Spikelets* 1–9 (infrequently –16) per branch, relatively widely spaced, more or less appressed along the rachis and not pectinate, relatively long, mostly 7–15 mm or more in length including the awns. *Body of the lemma of the lower (perfect) floret* (4–) 4.5–8 mm long. *Rudimentary florets* 1, rarely 2, the body with pointed lobes of tissue or the lobes lacking. *Rachilla* without a tuft of hair below the rudiment. *Caryopses* in most species narrowly ovate, elliptic, or oblong and 3.5–7 times as long as broad; embryo 50–70% as long as the endosperm.

TYPE SPECIES: *Bouteloua curtipendula* (Michaux) Torrey. BASIONYM: *Chloris curtipendula* Michaux.

A few exceptions to the general characterization of subgen. *Bouteloua* are noteworthy. In *B. juncea* the lower lemma averages only 4 mm long. Two rudiments commonly are present in *B. rigidiseta*, and in *B. megapotamica* there are 2–4 long-awned rudiments. In *B. aristidoides* the rachilla is hairy below the rudiment. In *B. chondrosioides* the spikelets are moderately pectinate and 9–16 per branch. *Bouteloua johnstonii* has moderately pectinate spikelets with 2 rudiments.

Bouteloua Lag. subgen. **Chondrosium** (Desvaux) Gould, stat. nov.

Chondrosium Desvaux, Nouv. Bull. Soc. Philom. Paris 2: 188. 1810.

Inflorescence branches 1–6, rarely more, typically 2–5 cm long including the spikelets. *Disarticulation* at the base of the spikelet, the branch rachis persistent. *Spikelets* 20–100 per branch, typically closely placed and spreading at a wide angle from the rachis (pectinate), relatively short, infrequently as much as 7 mm long. *Body of the lemma of the lower (perfect) floret* averaging 1.5–4.0 mm long. *Rudimentary florets* usually 2–3, the body of the lowermost rudiment with rounded membranous lobes. *Rachilla* with a tuft of hair below the lowermost rudiment. *Caryopses* mostly narrowly elliptic or obovate, 2–4 times as long as broad, embryo 70–90% as long as the endosperm.

TYPE SPECIES: *Bouteloua simplex* Lag.

Perhaps outstanding of the species with atypical characteristics are *B. eriopoda* and *B. kayi* which have infloresecence branches with relatively few, widely spaced and nonpectinate spikelets. The tuft of hairs at the base of the lower rudiment is absent in *B. kayi*.

KEY TO THE SPECIES

1. Inflorescence branches deciduous at maturity, the spikelets falling with the branch; spikelets all or mostly 1–16 per branch ..... I. Subgenus *Bouteloua*
1′. Inflorescence branches persistent, the spikelets disarticulating above the glumes; spikelets typically 20–60 per branch (see also *B. eriopoda* and *B. kayi* with spikelets 6–20 per branch) ..... II. Subgenus *Chondrosium*

I. Subgenus *Bouteloua*

2. Inflorescence branches all or mostly with 1 spikelet.
   3. Spikelet rudiment with 3 long awns, these equally developed; second glume shorter than the lowermost lemma.
      4. Inflorescences 1–5 cm long, usually with 8 to 20 branches; nerves of the lemma extending into short awns; spikelets erect-spreading, generally 0.5–1 cm long including the awns ..... 2. *B. juncea*
      4′. Inflorescence 8–15 cm long, usually with 20–80 branches; nerves of the lemma not extending into awns; spikelets spreading at right angles to the inflorescence axis or reflexed, typically more than 1 cm long including the awns ..... 1. *B. triaena*
   3′. Spikelet rudiment awnless or with only 1 well-developed awn; second glume as long as or exceeding the lowermost lemma.
      5. Attachment of spikelet 2–3 mm from the base of the branch rachis; looping stolons developed ..... 7. *B. pedicellata*
      5′. Attachment of the spikelet 0.5 mm or less from the base of the branch rachis; stolons not developed.
         6. Leaves relatively long, not or only slightly curved; leafy portion of the plant 15–30 cm or more high; flowering culms mostly 25–50 cm tall, not scapose; inflorescence commonly with 40–60 branches, these typically closely placed and strongly reflexed ..... 8a. *B. uniflora* var. *uniflora*
         6′. Leaves short, curved; leafy portion of the plant 6–12 cm high; flowering culms 20–30(–45) cm tall, scapose; inflorescence with 15–30(–40) branches, these relatively loosely arranged, often spreading at wide angles from the culm axis and not strongly reflexed ..... 8b. *B. uniflora* var. *coahuilensis*
2′. Inflorescence branches all or mostly with 2–15 spikelets.
   7. Inflorescence branches 15–80 per culm or if less than 15 then the branches, including the spikelets, less than 1 cm long ..... A
   7′. Inflorescence branches 1–13 per culm or if more than 13 the branches, including the spikelets, 1.5 cm or more long ..... AA

A

8. Plants annual, usually with long, trailing culms; awn of the rudiment 6–10 mm long; second glume and lemma about equal; plants of southern Mexico, Central and South America ..... 6. *B. disticha*
8′. Plants perennial.
   9. Rudiment with 3 equal or nearly equal awns; first glume about half as long as the second; middle inflorescence branches usually with 2–3 spikelets; states of Oaxaca and Nuevo León, Mexico, infrequent ..... 4. *B. distans*
   9′. Rudiment awns unequally developed when present, the central one longer than the lateral two; first glume more than half as long as the second when inflorescence branches with as few as 2–3 spikelets.
      10. Leaf blades 1–2(–2.5) mm broad, usually involute on drying; plant with stiffly erect culms, these never stoloniferous.
         11. Anthers yellow; ligules 0.5 mm or less long; Antilles ..... 5. *B. vaneedenii*
         11′. Anthers purple; ligules 1.0–1.5 mm long; southern New Mexico, western Texas, northern Mexico ..... 12. *B. warnockii*
      10′. Leaf blades, at least some, more than 2.5 mm broad or plants with stolons or stoloniferous culms.
         12. Plants with creeping rhizomes, stolons, or slender, decumbent or trailing culms, the culms not in large clumps.
            13. Plants stoloniferous, sod-forming; anthers dark purple; plants of Guanajuato and adjacent states of Mexico, growing on heavy, dark soils ..... 11. *B. purpurea*
            13′. Plants stoloniferous or not, when stoloniferous then the anthers not purple.
               14. Stolons absent, creeping rhizomes present; culms stiffly erect;

anthers red or orange (rarely yellow or purple); widespread in U.S. ---------- 14a. *B. curtipendula* var. *curtipendula*

14′. Stolons present or culms slender, decumbent and often rooting at the lower nodes; creeping rhizomes absent or less frequently present; anthers yellow, orange, or red; Mexico ---------- 14b. *B. curtipendula* var. *tenuis*

12′. Plants with stiffly erect culms in large or small clumps, the plant base "knotty" in some forms; stolons or creeping rhizomes not developed.

15. Culms typically with 4–7 nodes elevated above the base of the plant; sheaths and blades glabrous or more frequently pilose or hirsute; spikelets relatively small, the second glume 3–5(–6) mm long; secondary inflorescences frequently developed at the upper culm nodes; branches of the primary inflorescence mostly with 7–13 or more spikelets.

16. Anthers red or red orange, rarely yellow; spikelets glabrous or variously pubescent; body of the rudiment usually well developed, often protruding above the lemma of the fertile floret; southcentral Mexico to Guatemala ---------- 9. *B. media*

16′. Anthers yellow or pale orange; spikelets glabrous; body of the rudiment absent or greatly reduced; Gulf of California region ---------- 10. *B. reflexa*

15′. Culms with 1–2(–3) nodes elevated above the base of the plant; sheaths and blades usually glabrous except for ciliate margins and scattered hairs; spikelets relatively large, the second glume usually 6–8 mm long; secondary inflorescence not produced at the upper culm nodes; branches of the inflorescence mostly with 2–6 spikelets; anthers usually yellow or orange; southwestern United States to South America ---------- 14c. *B. curtipendula* var. *caespitosa*

AA

17. Spikelet with 2–4 long-awned rudiments; stoloniferous perennial of South America ---------- 19. *B. megapotamica*

17′. Spikelet with a single long- or short-awned rudiment.

18. Upper floret typically neuter, reduced to a cylindrical awn column and 3 awns of equal or nearly equal length; spikelets widely spaced on and appressed to the branch rachis.

19. Branches of the inflorescence widely spreading or deflexed at maturity, readily deciduous; inflorescence branch rachis sharply pointed at the base; short-lived annual of arid or semi-arid regions ---------- 21. *B. aristidoides*

19′. Branches of the inflorescence not widely spreading at maturity; inflorescence branch rachis not sharply pointed at the base; annual or perennial.

20. Glumes nearly equal, the first glume shorter than the second by 1 mm or less; plant perennial but flowering the first year; Cuba, the Bahamas, and Yucatán to South America ---------- 3. *B. americana*

20′. Glumes very unequal, the first glume shorter than the second by 2–4 mm; plant annual; Baja California ---------- 18. *B. annua*

18′. Upper floret well developed, perfect, staminate or neuter but not reduced to an awn column and 3 awns of equal or nearly equal length; spikelets closely spaced on and appressed to or spreading from the branch rachis.

21. Middle inflorescence branches with an average of 12–20 spikelets; culm bases firm, erect, without rhizomes; lemma of the lower floret 4.5–6 mm long, with 3 awns, the central one 2–3 mm long.

22. Lower floret with a tuft of hairs at the base ---------- 13. *B. williamsii*

22′. Lower floret without a tuft of hairs at the base ---------- 15. *B. repens*

21′. Middle inflorescence branches with 4–16 spikelets, when spikelets more than 11 per branch, then the culm base with a stout rhizome; lemma of the lower floret 4.5–8 mm long, with or without well-developed awns.

23. Culms from stout scaly rhizomes, these covered by more or less persistent, broad, flattened, light-colored leaf sheaths; lemma of the lower floret awnless or occasionally with short awns ---------- 16. *B. radicosa*

23′. Culms not from stout, scaly rhizomes covered by light-colored sheaths, the rhizomes when present slender, knotty, and dark colored.
24. Plants annual ---------- 17. *B. alamosana*
24′. Plants perennial.
25. Second glume glabrous or scabrous ---------- 15. *B. repens*
25′. Second glume hispid or ciliate.
26. Second glume scabrous-ciliate on the midnerve and the base of the lateral nerves, not hispid on the internerves ---------- 20. *B. rigidiseta*
26′. Second glume hispid on the internerves, at least below.
27. Leaf blades involute; second glume hispid only near the base ---------- 24. *B. johnstonii*
27.′ Leaf blades narrow but flat; second glume hispid to well above the middle.
28. Inflorescence branches usually 8–14 per culm and 5–8 mm long excluding the awns ---------- 23. *B. eludens*
28′. Inflorescence branches usually 3–7 per culm and 1 cm or more long excluding the awns ---------- 22. *B. chondrosioides*

II. Subgenus *Chondrosium*

29. Inflorescence a unilateral spike.
30. Plants annual ---------- 34. *B. simplex*
30′. Plants perennial.
31. Rachis of the spike extending well beyond the point of insertion of the terminal spikelet; second glume of at least some spikelets with papilla-based hairs.
32. Tuft of hairs not present at the base of the lowermost rudiment; culms mostly 15–40 cm tall, the base not firm or woody and the leaves not basally clustered ---------- 27. *B. hirsuta*
32′. Tuft of hairs present at the base of the lowermost rudiment; culms mostly 25–75 cm tall, with the leaves mostly in a basal cluster on a firm, almost woody base ---------- 28. *B. pectinata*
31′. Rachis of the spike not extending beyond the point of insertion of the terminal spikelet; second glume hairy or glabrous.
33. Rachis of the spike and the second glume glabrous or scabrous ---------- 26. *B. scorpioides*
33′. Rachis of the spike and the second glume pilose or hispid, often with long, papilla-based hairs ---------- 25. *B. gracilis*
29′. Inflorescence with 2 to several unilateral spicate branches.
34. Second glume of at least some spikelets hispid or hirsute with papilla-based hairs.
35. Rachis of the inflorescence branch extending well beyond the point of insertion of the terminal spikelet.
36. Tuft of hairs not present at the base of the lowermost rudiment; culms mostly 15–40 cm tall, the base not firm or woody and the leaves not basally clustered ---------- 27. *B. hirsuta*
36′. Tuft of hairs present at the base of the lowermost rudiment; culms mostly 25–75 cm tall, with the leaves mostly in a basal cluster on a firm, almost woody base ---------- 28. *B. pectinata*
35′. Rachis of the inflorescence branch not extending beyond the point of insertion of the terminal spikelet.
37. Inflorescence branches mostly 10–30; perennial ---------- 35. *B. elata*
37′. Inflorescence branches 7 or less; annual or perennial.
38. Lemmas ca. 2 mm long; inflorescence branches (2–)3–6, 1–1.5(–2) cm long; plants caespitose or stoloniferous but not rhizomatous ---------- 36. *B. parryi*
38′. Lemmas 4–5.5 mm long; inflorescence branches 2(1–4), mostly 2–4.5 cm long; plants usually rhizomatous ---------- 25. *B. gracilis*
34′. Second glume glabrous or hairy but lacking papillae or papillate hairs.

39. Culm internodes, at least the lower, wooly-pubescent.
    40. Second glume and branch rachis glabrous; plants stoloniferous ---------- 29. *B. eriopoda*
    40′. Second glume and branch rachis villous to lanate; plants not stoloniferous ---------- 30. *B. eriostachya*
39′. Culm internodes glabrous.
    41. Plants annual ---------- 33. *B. barbata*
    41′. Plants perennial.
        42. Inflorescence branches 2(1–4).
            43. Culms usually with 2–3 nodes; base of the plant firm but not woody ---------- 25. *B. gracilis*
            43′. Culms usually with 4–5 nodes; base of the plant firm and relatively woody ---------- 39. *B. breviseta*
        42′. Inflorescence branches 3–30.
            44. Plant base with stout rhizomes.
                45. Second glume 3–3.5 mm long; rachilla with a dense tuft of hairs at the base of the rudiment ---------- 37. *B. chasei*
                45′. Second glume 2–2.5 mm long; rachilla without a dense tuft of hairs at the base of the rudiment ----- 38. *B. karwinskii*
            44′. Plant base not rhizomatous.
                46. Lemma of the lower floret glabrous, with an awn mostly 5 mm or more long.
                    47. Inflorescence branches mostly 8–20 ---------- 32. *B. kayi*
                    47′. Inflorescence branches 3–7 ---------- 31. *B. trifida*
                46′. Lemma of the lower floret pubescent below, with an awn 0.5–3 mm long ---------- 33. *B. barbata*

1. **Bouteloua triaena** (Trinius) Scribner, Proc. Acad. Nat. Sci. Philadelphia 1891: 307. 1891.—FIG. 1.

Triaena racemosa H.B.K., Nov. Gen. Sp. Pl. 1: 179. 1816, not *Bouteloua racemosa* Lag. TYPE: Mexico, "inter Guanaxuato Mexicanorum et Villalpando," *Humboldt & Bonpland*. *Triathera racemosa* (H.B.K.) Desvaux, Opusc. Sci. Phys. Nat. 72. 1831.
Eutriana triaena Trinius, Gram. Unifl. 239. 1824, based on *Triaena racemosa* Kunth. *Atheropogon triaena* (Trinius) Sprengel, Syst. Veg. 1: 293. 1825.

Tufted *perennial*. *Culms* slender and erect, 20–50 cm tall or, in moist shady sites, weak and trailing, as much as 80–100 cm long. *Leaves* glabrous, except for the short-pubescent ligule and a few longer hairs in the vicinity of the ligule. *Blades* long, thin, mostly 1–3 mm broad. *Inflorescence* 8–15 cm long, with usually 20–80 closely placed floriferous branches, *branches* typically spreading at a wide angle or reflexed, the rachis short, subsetaceous, and bearing a single spikelet. *Glumes* glabrous and awnless, the first usually 2–3 mm long, the second about twice as long. *Lemma* smooth and shiny, scabrous or short pubescent, awnless, usually about 2 mm longer than the second glume. *Palea* slightly shorter than lemma, narrow at the apex. *Rudiment* reduced to an awn column about 3 mm long and 3 equally developed awns commonly 1–1.5 cm or more long. *Glumes*, *lemmas*, and *awns* yellowish green to purple. *Anthers* yellow or orange. *Caryopsis* about 3 mm long, narrowly ovate-elongate.

HABITAT: Most commonly growing in rocky, dry soil on exposed or partially shaded slopes, often associated with brush and scrub trees. In Chiapas, collected on a steep canyon wall in tropical deciduous forest. The altitudinal range of this short-lived perennial is from about 35 m (in Yucatán) to over 2,500 m (in Puebla and Chiapas).

DISTRIBUTION: Mexico (Chiapas, Guerrero, Hidalgo, México, Morelos, Michoacán, Oaxaca, Puebla, Sinaloa, and Yucatán) and Guatemala.

2. **Bouteloua juncea** (Desvaux ex Beauvois) Hitchcock, Contr. U.S. Natl. Herb. 17: 343. 1913.—FIG. 2.

Triathera juncea Desvaux ex Beauvois, Ess. Agrost. 40, 179. 1812. TYPE: Hispaniola, ex Herb. *Desvaux* (US, holotype fragment). *Eutriana juncea* (Desvaux ex Beauvois) Trinius, Gram. Unifl. 238. 1824. *Triaena juncea* (Desvaux ex Beauvois) Griffiths (in part), Contr. U.S. Natl. Herb. 14: 354. 1912.
Eutriana ledebouri Trinius, Gram. Unifl. 238. 1824. TYPE: "W. I., Ins. S. Doming." "in Herbar. Rudolphii."
Atheropogon domingensis Sprengel, Syst. Veg. 1: 293. 1825. TYPE: "Hispaniola."

Low tufted *perennial*, frequently developing stolons. *Culms* slender, delicate, 5–30 cm long. *Ligule* ciliate, ca. 0.5 mm long. *Blades* involute or less frequently flat, rather stiffly curving, 1–4 cm long. *Inflorescence* 1–5 cm long, usually with 8–20 erect-spreading *branches*; branches subsetaceous, ca. 1 mm long, with a single spikelet. *Glumes* broad at the base, acute or acuminate, the first ca. 1 mm long, the second 1.8–3 mm long. *Lemma of the lower floret* 1–2 mm longer than the second glume, glabrous, scabrous or sparsely strigose, the 3 nerves usually prolonged as short, stout awns. Rudiment reduced to an awn column and 3 equally developed awns 6–9 mm long. *Caryopsis* slender, tapering at both ends, ca. 1.5 mm long.

HABITATS: On sandy shores and sandy flats near the ocean.

DISTRIBUTION: Cuba (Oriente), Haiti, Dominican Republic (Agua, Barahona, Monte Christi), and Puerto Rico.

Bouteloua juncea appears closely related to *B. triaena* from which it differs mainly in the smaller stature, the awned lemmas, the extremely short inflorescence axis, and the small erect-spreading spikelets.

3. **Bouteloua americana** (L.) Scribner, Proc. Acad. Nat. Sci. Philadelphia 1891: 306. 1891.—FIG. 3.

Aristida americana L., Syst. Nat., ed. 10, 2: 879. 1759. TYPE: Jamaica, *Patrick Browne* (type in LINN according to Griffiths [1912]). *Triathera americana* (L.) Desvaux, Nouv. Bull. Soc. Sci. Philom. Paris 2: 188. 1810. *Dineba americana* (L.) Beauvois, Ess. Agrost. 98, 160, *pl. 16, figs. 1–3*. 1812. *Heterostega americana* (L.) Desvaux, J. Bot. Appl. 1: 68. 1813. *Bouteloua litigiosa* Lag., Gen. & Sp. Nov. 5. 1816, based on *Aristida americana* L. *Atheropogon americanus* (L.) Fournier, Mex. Pl. Gram. 2: 139. 1886. *Aristida adscensionis* L. var. *americana* (L.) Kuntze, Rev. Gen. Pl. 3(3): 340. 1898.
Aristida antillarum Poir. in Lam., Encycl. Suppl. 1: 451. 1810. TYPE: Antilles. *Chaetaria antillarum* (Poir.) Beauvois ex Roemer & Schultes, Syst. Veg. 2: 395. 1817. *Atheropogon antillarum* (Poir.) Sprengel, Syst. Veg. 1: 294. 1825. *Eutriana antillarum* (Poir.) Steudel, Syn. Pl. Glum. 1: 217. 1854.
Bouteloua humboldtiana Grisebach, Mem. Amer. Acad. Arts, n. s., 8: 532. 1862. TYPE: Cuba, Oriente, *Wright 734* (GOET, holotype, not seen; NY, P, isotypes).
Bouteloua porphyrantha Wright, Anales Acad. Ci. Méd. Habana 8: 201. 1871. TYPE: Cuba, Oriente, *Wright 739* (G, P, US, isotypes. Photograph of holotype in US shows two plants of *B. americana* and one shoot of *B. repens* var. *repens*. Hitchcock [1936] referred the Cuban collections *Wright 734*, *739*, and *3816* to *B. heterostega* [*B. repens*], but isotypes of *734* [G, NY, P], *739* [P, US], and *3816* [GH], are specimens of *B. americana*).
Bouteloua elatior Grisebach, Fl. Brit. W. I. 537. 1864. TYPE: Lesser Antilles, Antigua, *Wullschlagel 619* and *660* (syntypes, fragments in US).

FIGURES 1–3. Distribution of *Bouteloua* species.—1. *B. triaena*.—2. *B. juncea*.—3. *B. americana*.

Plants *perennial*, but flowering the first year and often appearing annual. *Culms* glabrous, many noded, mostly weak, decumbent or trailing and freely branching in age, from 8 cm or less long in depauperate plants to more than 1 m long in forms with vigorous, trailing culms. *Sheaths* shorter than the internodes,

glabrous or with a few hairs on the margins near the apex. *Blades* mostly 2–4 mm broad, glabrous or more commonly ciliate along the lower margins with stiff, pustula-based hairs, occasionally sparsely hirsute on one or both surfaces. *Inflorescence* well exserted or partially included in the upper sheath, usually with 5–12 slender, spicate branches mostly 1.5–4 cm long; *branches* deciduous with the spikelets intact or less frequently remaining attached to the main axis until after the spikelets disarticulate above the glumes. *Spikelets* slender, mosly 5–10 per branch, typically widely spaced on and appressed to the rachis, with a single reduced floret above perfect one. *Glumes* glabrous, broad, acute, acuminate, or short awned, 3.5–5 (occasionally –6) mm long, the first slightly shorter than the second. *Lower floret* slender; *lemma* short awned, mostly 4.5–7 mm long excluding the awns, with a tuft of stiff white hairs at the base, the body glabrous or infrequently puberulent in lines; *palea* narrow, longer than the body of the lemma, the 2 nerves extended as short awns. *Upper floret* typically reduced to a cylindrical awn column with equal or nearly equal awns that diverge at the same point. *Caryopsis* narrowly ovate, 3–3.5 mm long.

HABITAT: Mostly on sandy shores along the ocean or sandy inland sites at low elevations. In South America this species grows from near sea level to moderately high elevations.

DISTRIBUTION: From the Bahama Islands, Cuba and the Yucatán Peninsula, southward through the Caribbean and Central America to Colombia, Venezuela, Guyana, and Brazil (Ceará, Maranhão, Pernambuco, and Rio Grande do Norte).

Bouteloua americana is similar to, and probably closely related to, *B. juncea* which occupies the same habitats in the Caribbean region. South American plants of *B. americana* growing at moderately high elevations tend to be strongly perennial, with stiffly erect culms. Although the upper floret typically is reduced to a cylindrical awn column with 3 awns, in *Tamayo* 2288 (UC, US) from Laderas de San Pablo, Mérida, Venezuela, a palea is present in the upper floret.

4. **Bouteloua distans** Swallen, Contr. U.S. Natl. Herb. 29: 401. 1950. TYPE: Mexico, Oaxaca, ca. 170 km N of Oaxaca City, 13 Dec. 1945, *J. A. Jenkins & F. Hernandez X. X-808* (US, holotype; CHAPA, US, isotypes).—FIG. 4.

Caespitose *perennial*. *Culms* 38–60 cm tall. *Sheaths* longer than the internodes, sparsely to densely papillose-villous. *Ligule* a minute fringe of hairs. *Blades* flat, 1.5–3.5 mm broad, glabrous or sparsely ciliate on the lower margins, becoming curled in age. *Inflorescence* 12–19 cm long, usually with 20–50 branches, these rather consistently with 2–3 spikelets. *Spikelets* 8–9 mm long with glabrous, relatively narrow, attenuate or subattenuate, purple-colored glumes and lemma. First glume about half as long as the second. *Second glume* and *lemma* about equal, both awnless. *Rudiment* moderately well developed, with 3 equal or nearly equal awns on a narrow, stipelike base, the awns mostly 4–6 mm long. *Caryopsis* not seen.

HABITAT: On rocky slopes at moderately high altitudes in oak-juniper woods.

DISTRIBUTION: Mexico. Known only from the type collection and from near

Oaxaca (*Beetle M-3219* [TAES], and from Iturbe, Nuevo León (*Brunken & Perino 203* [TAES]).

5. **Bouteloua vaneedenii** Pilger ex Urban, Symb. Antill. 6: 2. 1909. TYPE: Lesser Antilles, Anguilla, *Boldingh 3512B* (US, holotype fragment).—FIG. 5.

Caespitose *perennial* with numerous slender culms in a dense clump from a firm, "knotty" base. *Culms* mostly 30–40 cm tall but varying from 20–50 cm. *Ligule* a minute fringe of hairs 0.25 mm or less long. *Blades* long, flexible, filiform, 0.5–1.5 mm broad, involute or less frequently flat, glabrous. *Inflorescence* mostly with 15–35 branches, these bearing 1–5 (usually 2) spikelets. *Spikelets* 4–6 mm long. *Glumes* purple tinged, the first 2–4 mm long, the second 3.5–5 mm long. *Lemma* pale green, about as long as the second glume, the 3 nerves extended as short awns. Rudiment minute to moderately well developed, the central awn to 2.5 mm long. *Caryopsis* not seen.

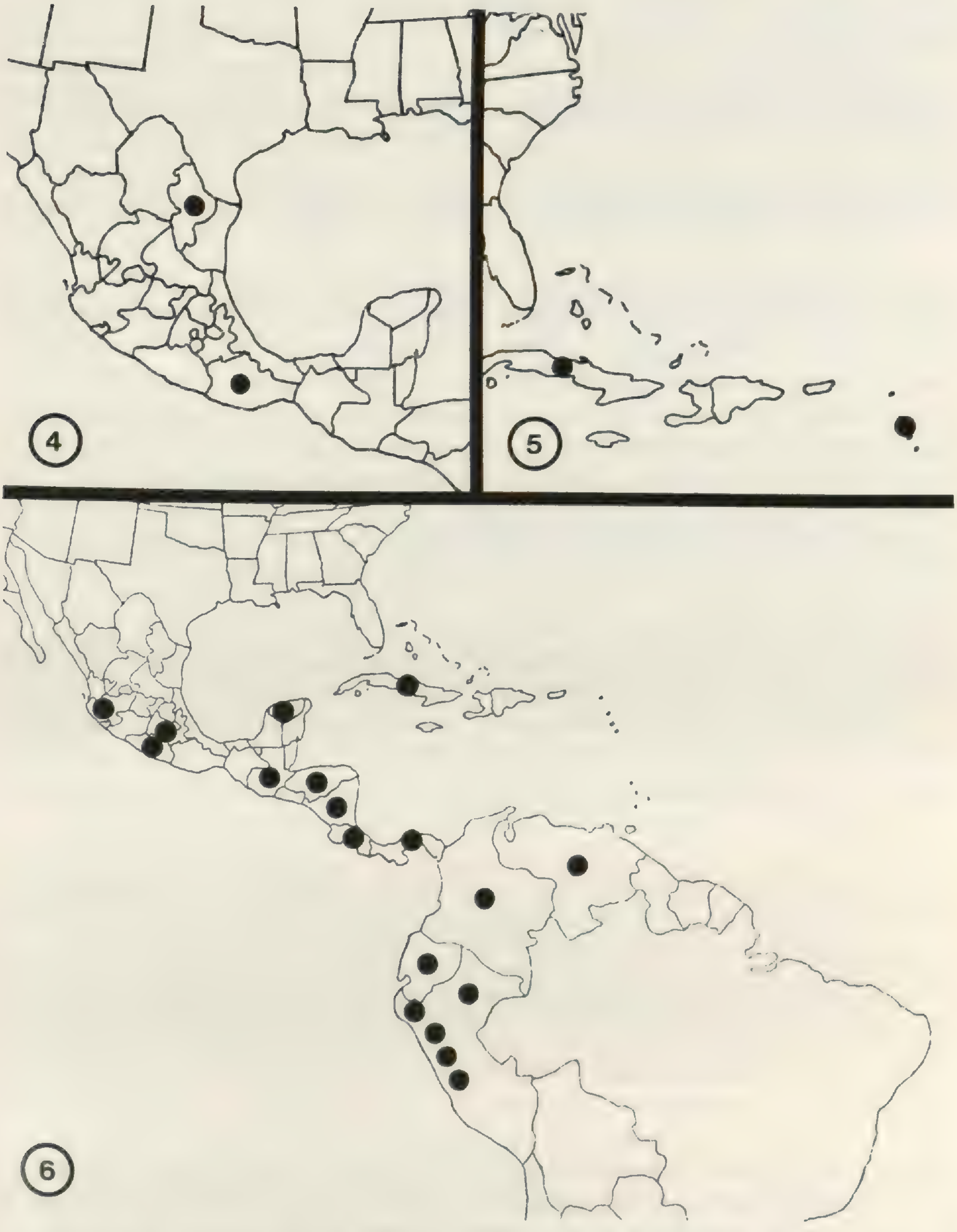
HABITAT: On rocky, open shores. One of the *Ekman* collections from Cuba bears the notation "in dry limestone littoral rocks" and the other has a more recent note "on Miocene limestone."

DISTRIBUTION. Known to me only from Pastelillo, Cuba (*Ekman 1013* [GH, TAES]), Anguilla (*Boldingh 3512B* [US]), and Guadeloupe (*Galla 2542* [NY]). *Hitchcock* (1930) reports this species from Venezuela based on *Boldingh 3512* but I have not seen this specimen.

6. **Bouteloua disticha** (H.B.K.) Bentham, J. Linn. Soc. Bot. 19: 105. 1881.—FIG. 6.

Polydon distichum H.B.K., Nov. Gen. Sp. Pl. 1: 175. 1816. TYPE: Ecuador, Quito, *Humboldt & Bonpland*. *Eutriana polydon* Trinius, Gram. Unifl. 242. 1824, based on *Polydon distichum* H.B.K. *Atheropogon distichus* (H.B.K.) Sprengel, Syst. Veg. 1: 294. 1825.
Eutriana pilosa Hook. f., Trans. Linn. Soc. London 20: 173. 1847. TYPE: Galapagos, Albemarle Isl. *Macrae*. *Bouteloua pilosa* (Hooker f.) S. Watson, Proc. Amer. Acad. Arts 18: 1883.
Eutriana gracilis Hook. f., Trans. Linn. Soc. London 20: 175. 1847, not *Bouteloua gracilis* Hook., nor Lag. TYPE: Argentina, Tucuman, *Tweedie*.
Eutriana mucronata F. Areschoug., Kongl. Svenska Fregatten Eugenies Resa, Bot. 3: 118. 1910. TYPE: Ecuador, "in insula Puna," *Andersson*.
Bouteloua piurensis Pilger, Repert. Spec. Nov. Regni Veg. 17: 447. 1921. TYPE: Peru, Dept. and Prov. Piura, *Weberbauer 5961*.

Coarse *annual*. *Culms* weak, usually decumbent trailing or stoloniferous, 40–100 cm or more long. *Leaves* glabrous or sparsely hirsute or pilose. *Ligule* ciliate, ca. 0.5 mm long. *Blades* long and flat, mostly 3–6 mm broad. *Inflorescence* with 15–45 branches, these mostly with 3–4 spikelets crowded on the basal ¼ of a flattened rachis. *Spikelets* 6–8 mm long excluding the awns, greenish or yellowish green. *First glume* 3–4 mm long, setaceous, the second mostly 4.5–7 mm long, acute or apiculate from a slightly notched apex. *Lemma of the lower floret*, including the awns, as long as the second glume or slightly shorter, the 3 nerves terminating in short awns. *Anthers* orange to deep orange red. *Upper floret* rudimentary, the lemma with a greatly reduced body and a central awn 0.6–1 cm long; two short lateral awns often present. *Caryopsis* not seen.



FIGURES 4–6. Distribution of *Bouteloua* species.—4. *B. distans*.—5. *B. vaneedenii*.—6. *B. disticha*.

HABITAT: In a wide variety of habitats but most commonly on dry, open or partially shaded slopes, mostly at elevations of 300–2,000 m.

DISTRIBUTION: Cuba and southern Mexico (Yucatán, Morelos, Jalisco, Guerrero), south through Central America to Venezuela, Ecuador, the Galápagos Is-

lands, and Peru (La Libertad, Lambayeque, Lima, Loreto, Negritos, Piura, and and Tumbes).

Plants with stolons to 2 m long have been noted both in Mexico (Morelos, near Jojutla *Reeder & Reeder 4151* [TAES]) and in Honduras (Zamorana, *Gould 9480* [TAES]).

7. **Bouteloua pedicellata** Swallen, N. Amer. Fl. 17: 627. 1939. TYPE: Mexico, Puebla, Chalchicomula, *Hitchcock 6302* (US, holotype).—FIG. 7.

Low tufted *perennial*, developing looping stolons as much as 45 cm long. *Culms* mostly 15–25 cm tall. *Ligule* a dense fringe of hairs 0.5–0.8 mm long. *Blades* 2–5 cm long, involute, grayish green. *Inflorescence* with mostly 10–20 branches; branches stiffly spreading or reflexed, regularly bearing a single spikelet attached 2–3 mm from the base of a flat, ciliate rachis. *Glumes* broad and firm, acute, awnless, slightly scabrous on the keel, the first 3–4 mm long, the second about twice as long. *Lemma* and *palea* glabrous, awnless or nearly so, similar in texture and about equal in length, thinner than the glumes and slightly shorter than the second glume. *Anthers* bright yellow. *Rudiment* greatly reduced, generally consisting of a single short awn, this not exserted from the spikelet. *Caryopsis* not seen.

HABITAT: On dry, rocky slopes at high elevation, the type collection from 3,000 m.

DISTRIBUTION: Mexico. Known from four collections, the type (*Hitchcock 6302*) from Chalchicomula, Puebla, *Weaver 873* (TAES, US) from near Lago Salido, Puebla, *Hitchcock 6474*, in part (US) from Esperanza, Puebla, and *Sohns 629* (CHAPA, US) from near the Huamantla-El Carmen road, Tlaxcala.

8. **Bouteloua uniflora** Vasey, Bot. Gaz. (Crawfordsville) 16: 26. 1891. TYPE: United States, Texas, Crockett County, *Nealley 222* (US, holotype; GH, isotype).

Tufted perennial lacking rhizomes or stolons. *Culms* glabrous, slender, stiffly erect. *Leaves* essentially glabrous or minutely scabrous, usually with a few long hairs in the vicinity of the ligule and on the margins of the blades. *Ligule* a minute fringe of hairs. *Blades* narrow and flat but usually involute on drying, 1–2 mm broad. *Inflorescence branches* bearing 1 spikelet (rarely 2) near the base of a stiff, narrow rachis ca. 5 mm in length. *Glumes* broad, thin, acute or slightly notched and minutely apiculate, usually scabrous on the midnerve, the first 3–4 mm long, the second 7–8 mm long. *Lemma* slightly shorter than the second glume, acute or minutely notched, awnless. *Palea* similar to the lemma in texture but slightly shorter. *Anthers* bright lemon yellow, 2.5–3 mm long. *Rudiment* absent or minute and represented by 1 or 3 short bristles. *Caryopsis* narrowly ovate, ca. 3 mm long and ca. 7 times as long as broad.

8a. **Bouteloua uniflora** var. **uniflora**—FIG. 7.

Culms mostly 40–60 cm tall, leafy well above the base. *Leaf blades*, at least

some, 12–16 cm long, the larger ones straight or only slightly curving. *Inflorescence* characteristically with 50–70 or more closely placed, strongly reflexed branches.

HABITAT: Plants of fertile, usually rocky soils, in open, dry or moderately humid sites, mostly at elevations of 300–1,000 m.

DISTRIBUTION: Most frequent on the Edwards Plateau of central Texas, ranging westward to Hudspeth and Brewster counties and southward to northern Coahuila, Mexico.

8b. **Bouteloua uniflora** var. **coahuilensis** Gould & Kapadia, Brittonia 16: 191. 1964. TYPE: Mexico, Coahuila, 40 km SW of Saltillo, *Gould 10300* (TAES, holotype; DS, GH, TEX, UC, US, isotypes).—FIG. 8.

Leaves short, curved, in a basal tuft 6–12 cm high. *Flowering culms* scapose, mostly 20–40 cm tall. *Inflorescence* with 15–30 (–40) spicate branches, these loosely arranged and often widely spreading.

HABITAT: Dry, rocky, open, pastured slopes, at elevations of 300–2,000 m.

DISTRIBUTION: Mexico. At scattered localities in central Coahuila and in southern Nuevo León just east of Galeana.

At the type locality, plants of this taxon were observed growing with late-flowering, depauperate plants of *B. curtipendula* var. *caespitosa*. The latter were readily distinguishable by their orange anther color, slightly broader blades, and firmer, more knotty plant base.

9. **Bouteloua media** (Fournier) Gould & Kapadia, Brittonia 16: 196. 1964.—FIG. 9.

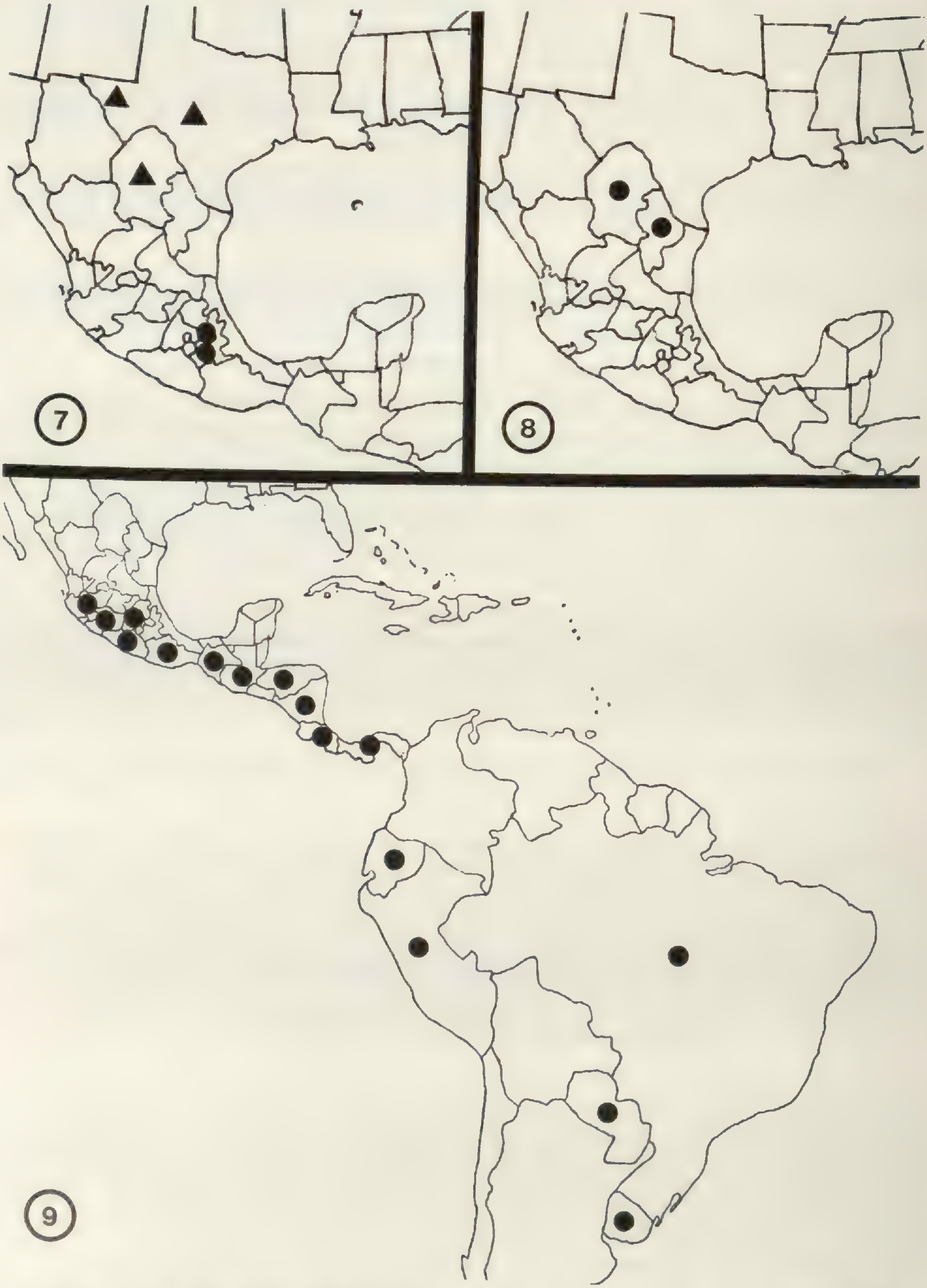
Atheropogon medius Fournier, Mex. Pl. Gram. 2: 139. 1889. TYPE: Mexico, "between T. Miguel and Sadani," *Liebmann 581* (US, holotype).

Bouteloua pringlei Scribner, U.S.D.A. Div. Agrostol. Circ. 30: 4. 1901. TYPE: Mexico, Guerrero, above Iguala, *Pringle 8374* (US, holotype; GH, NY, TAES, isotypes).

Bouteloua brasiliensis Ekman, Ark. Bot. 10: 29, *pl. 4, 6*. 1911. TYPE: Brazil, Matto Grosso, Cuiabá, "locis glareosis ad marginum silvulae, in fruticetis etc. legit *G. O. Malme*, 23. 4. 03, sub numero *3106* Exp. II Regn." (US, isotype).

Bouteloua latifolia Swallen, N. Amer. Fl. 17: 631. 1939. TYPE: Mexico, Morelos, "Hills near Yautepec," *C. G. Pringle 11217* (US, holotype; GH, TAES, isotypes).

Caespitose *perennial*, often with a "knotty" base but without creeping rhizomes. *Culms* stiffly erect, 80–200 cm tall under favorable growing conditions but occasionally much shorter, usually with 5–7 or more purple nodes, characteristically branching at one or more of the upper nodes to produce lateral as well as terminal inflorescences. *Culm leaves* well developed. *Sheaths* glabrous, sparsely hairy with long or short hairs (these often papilla based), or lanate with long soft hairs. *Ligular hairs* short, rarely as much as 0.5 mm long. *Blades* glabrous or variously pubescent, long and flat, 4–9 mm broad. *Primary inflorescences* bearing 7–15 closely placed branchlets, the upper branches short and with fewer spikelets, the lower branches often as much as 4–6 cm long and with 20 or more spikelets. *Slender secondary inflorescences* commonly developed at the culm nodes below the terminal one, these shorter than the primary, with more slender axes and shorter,



FIGURES 7–9. Distribution of *Bouteloua* species.—7. *B. pedicellata* (solid circles) and *B. uniflora* var. *uniflora* (solid triangles).—8. *B. uniflora* var. *coahuilensis*.—9. *B. media*.

fewer-flowered branches. *Spikelets* 4–6 mm long excluding the awns. *First glume* narrowly acute, attenuate or setaceous from a slightly broadened membranous base, the second broadly lanceolate to acute or acuminate, 3.4–4.5 mm long. *Lemma of the lower floret* slightly longer than the second glume, membranous between the 3 nerves which project as short awns. *Glumes* and *lemma* glabrous, scabrous, or short-pubescent. *Anthers* typically bright red or red orange. *Upper floret* rudimentary but usually well developed, the lemma with a large membranous body and aristate teeth that generally equal or surpass the tip of the lower lemma, the awns variable in length and irregular in development, usually 3–8 mm long but occasionally shorter. *Caryopsis* slender, tapering to both ends, mostly 2.2–2.5 mm long.

HABITAT: On open or partially shaded slopes and cliffs, often in or associated with underbrush, usually in fertile, loamy soils, at 300–3,000 m elevation.

DISTRIBUTION: Southern Mexico (Chiapas, Guerrero, Jalisco, México, Michoacán, Morelos, Oaxaca), Central America, Brazil, Ecuador, Peru, Paraguay, and Uruguay.

Bouteloua media is the tallest and most robust of the several known diploids of the *B. curtipendula* complex. The species is characterized by the firm knotty plant base, the frequently pubescent leaves, the reduced lateral inflorescences often produced below the terminal one, and the relatively small spikelets. Plants of South America tend to have shorter inflorescence branches with fewer spikelets. This taxon and the closely related diploid *B. reflexa* probably have contributed the tall, stiff culm characteristic to the series of populations referred to *B. curtipendula* var. *caespitosa*.

10. **Bouteloua reflexa** Swallen, N. Amer. Fl. 17: 632. 1939. TYPE: Mexico, Sinaloa (?), Lodiego, *Palmer 1655* (US, holotype; ARIZ, GH, US, isotypes). —FIG. 10.

Bouteloua acuminata Griffiths, Contr. U.S. Natl. Herb. 14: 406. 1912. Griffiths cited *Atheropogon acuminatus* Fournier as a basionym but described and figured *Palmer 1655*, the type of *B. reflexa* (*Atheropogon acuminatus* Fournier = *B. curtipendula* var. *caespitosa* Gould & Kapadia).

Plants *perennial* from a hard, knotty base. *Culms* stiffly erect, 60–120 cm or more tall, with numerous (4–9) nodes and internodes. *Ligules* membranous, often ciliate, 1–2 mm long. *Blades* long, flat, narrow, mostly 2–6 mm broad, usually glabrous except for a few long, papilla-based cilia at the base. *Inflorescence* 15–30 cm long, with usually 40–100 reflexed or spreading branches; branches progressively shorter from the uppermost to the basal branch, typically bearing 5–9 (–11) small, often widely spaced spikelets, these most frequently with only the terminal one or two spikelets fertile and the others variously reduced or rudimentary. *Spikelets* pale green, straw colored, or yellowish brown, rarely purple tinged. *Glumes* acuminate or subacuminate, the first 2–3 mm long, the second slightly longer. *Lemma* 4–5 mm long, slightly or greatly exceeding the second glume, the 3 nerves extended into short stout awns. *Anthers* orange. *Rudiment* poorly developed, the lateral awns minute or absent, the central awn to 4.5 mm long. *Caryopsis* slender, commonly ca. 2.5 mm long.

HABITAT: On exposed, rocky bluffs and slopes at low elevations.

DISTRIBUTION: Western Mexico, in Baja California Sur, islands of the Gulf of California and regions of Sonora and Sinaloa adjacent to the Gulf.

11. **Bouteloua purpurea** Gould & Kapadia, Brittonia 16: 197–198. 1964. TYPE: Mexico, México, 30 mi NW of Tepeji del Río, *Gould 10211* (TAES, holotype; GH, NY, TEX, UC, US, isotypes).—FIG. 11.

Perennial. Erect flowering *culms* mostly 20–60 cm tall, developed singly or in small clusters from looping stolons, these to 1 m or more in length. *Leaves* mostly in a basal tuft, glabrous or sparsely hispid or ciliate. *Ligule* a fimbriate membrane 0.4–0.8 mm long. *Blades* flat, linear, 1.5–3.0 mm broad, not curling in age. *Inflorescence* usually 12–20 cm long, with 30–50 branches, the branch rachis ca. 5 mm long, bearing (1–) 3–5 (–7) spikelets, these 5–7 mm long. *Glumes* purple tinged, glabrous or minutely scabrous on midnerve, the first narrow, acuminate, about ⅔ as long the second, the second broad, acute, 5–7 mm long, equal to or slightly surpassing the lemma. *Lemma* thin, usually purple tinged, acute at the apex, with the nerves prolonged as minute mucro. Anthers 3–4 mm long, deep purple or maroon purple. *Rudiment* highly variable in development, usually minute or absent but occasionally with a body to 3 mm long and an awn to 5 mm long. *Caryopsis* not seen.

HABITAT: Rich, rocky, heavy, black soils, at elevations of 1,800–2,300 m.

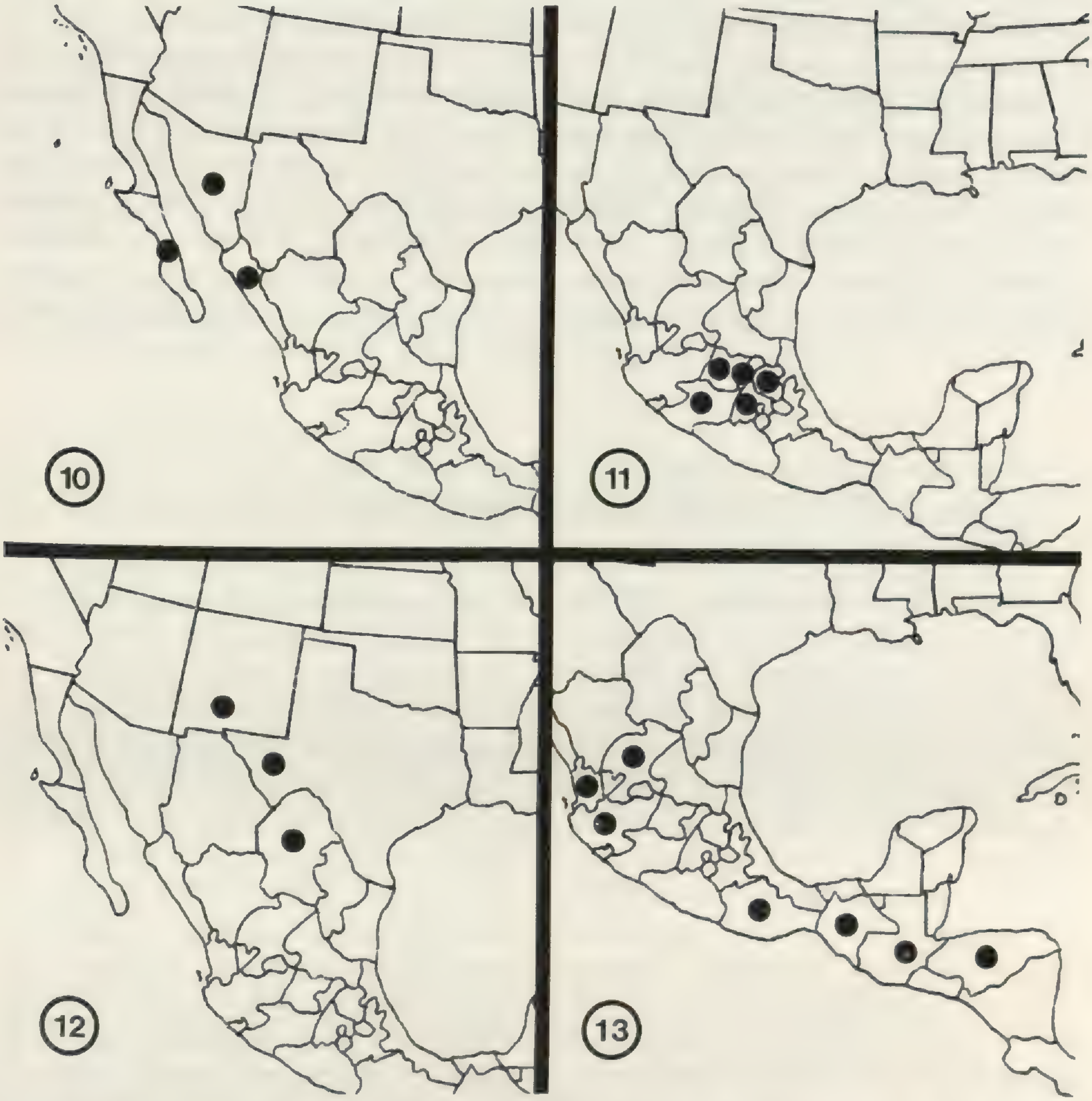
DISTRIBUTION: Southcentral Mexico, reported from the states of Guanajuato, Hidalgo, México, Michoacán, and Queretaro.

Bouteloua purpurea is a sod-forming grass that grows mainly in rough, rocky areas on the black clayey soils characteristic of much of the state of Guanajuato and adjacent areas. Most of these soils now are under cultivation and it can be assumed that *B. purpurea* once was much more abundant than at present.

The two chromosome counts reported for this species both are tetraploid ($2n = 40$) but the diploid form ($2n = 20$) is to be looked for. In both collections for which chromosome counts were obtained, prophase and metaphase figures of PMC division I regularly showed numerous multivalents; the diakinesis figured by Gould & Kapadia (1964) shows 9 quadrivalents and 2 bivalents. The strong tendency for multivalent formation suggests an autoploid origin for the tetraploid plants.

12. **Bouteloua warnockii** Gould & Kapadia, Southw. Naturalist 7: 176. 1962. TYPE: United States, Texas, Culberson Co., 2 mi W of Kent, *Gould & Kapadia 9533* (TAES, holotype; MICH, MO, SMU, SRSC, TEX, UC, US, isotypes).—FIG. 12.

Plants *perennial*, caespitose, the culms in tufts mostly 4–10 cm in diameter. *Culms* 20–35 (–50) cm tall, stiffly erect. *Leaves* bluish green, more or less glaucous, glabrous except for long and short hairs in the ligular area and a few long pustular-based hairs on the basal margins of the blades. *Ligule* a ring of hairs 1–1.5 mm long. *Blades* 1–1.5 (–2.5) mm broad, 5–15 (–25) cm long, erect or stiffly



FIGURES 10–13. Distribution of *Bouteloua* species.—10. *B. reflexa*.—11. *B. purpurea*.—12. *B. warnockii*.—13. *B. williamsii*.

curving, tapering to a fine tip, involute on drying. *Inflorescence* well exserted, usually 5–10 cm long and with 9–15 (–25) rather widely spaced spicate inflorescence branches, the branch rachis scabrous, 4–5.5 mm long, usually bearing 2–6 spikelets on the basal ¼ to ⅓. *Spikelets* 5–6.5 mm long. *Glumes* and *lemma* green, often with a purplish or brownish cast. *First glume* slightly shorter than the second, both usually shorter than the lemma. *Anthers* dark purple. *Rudiment* well developed, usually about as long as the lemma, awned but the awns only slightly or not at all exserted. *Caryopsis* narrowly ovate, 3.2–3.6 mm long, rounded at the apex and pointed at the base.

HABITAT: On exposed limestone ledges, dry plateau tops, and dry slopes below limestone outcrops, mostly at 1,300–1,500 m elevation.

DISTRIBUTION: Texas (Culberson, El Paso, Hudspeth, and Jeff Davis counties), New Mexico (Dona Ana Co.), and Mexico (northern Coahuila).

Bouteloua warnockii is remarkably similar in morphological characteristics to *B. vaneedenii*, a presumed diploid of the Caribbean region. Differences between the two mainly are in anther color, ligule length, and the presence of a few long hairs on the lower margins of the *B. warnockii* leaf blade. Although *B. warnockii* appears to be basically diploid, chromosome numbers reported for the species range from $2n = 21$ to 40 and the exact diploid number ($2n = 20$) has not been recorded. The aneuploid chromosome series in *B. warnockii* is believed to reflect hybridization between this taxon and *B. curtipendula* var. *caespitosa*. The two grow together, frequently intermingled, throughout the known range of *B. warnockii*.

13. **Bouteloua williamsii** Swallen, Ceiba 4: 285. 1955. TYPE: Honduras, El Paraíso, near Las Mesas, 900 m, *L. O. Williams 16902* (US, holotype; F, UC, WIS, isotypes).—FIG. 13.

Perennial. *Culms* slender, 35–90 cm tall, stiffly erect and unbranched from a firm tufted base. *Leaves* mostly basal, nearly glabrous to conspicuously hirsute; *blades* flat, filiform, mostly 1.5–2.5 mm broad, those of the basal clump 10–25 cm long, the upper shorter. *Inflorescence* with 7–14 branches alternating on either side of the angular, flattened main axis; branches 2–4 cm long, bearing 9–20 or more closely placed spikelets; *branch rachis* scabrous to puberulent, often with a tuft of hairs at the base of each spikelet. *Spikelets* 2-flowered, the lower perfect, the upper small and narrow, staminate or neuter. Glumes broad, acuminate, the first 2.5–4.5 mm long, the second 4.5–6 mm long. *Lemma of the lower floret* firm, with a body usually 4–6 mm long, glabrous or sparsely puberulent on the back and with a tuft of hairs at the base, the nerves extended as awns, the central awn mostly 2–3 mm long, the lateral awns shorter. *Palea of the lower floret* slightly longer than the lemma, puberulent between the minutely awn-tipped nerves. *Lemma of the upper floret* glabrous or minutely puberulent, usually with a tuft of silvery hairs at the base, with a stout central awn 4–7 mm long from a notched apex. *Caryopsis* not seen.

HABITAT: On dry, rocky slopes, in brushy or exposed sites at 800–2,200 m elevation.

DISTRIBUTION: Mexico (Chiapas, Jalisco, Nayarit, Oaxaca, Zacatecas), Guatemala, and Honduras.

In Central America *B. williamsii* is sympatric with *B. americana*, *B. repens*, and *B. alamosana*. There is evidence that in Mexico it hybridizes with both *B. repens* and *B. radicosa* (Gould, 1969).

14. **Bouteloua curtipendula** (Michaux) Torrey, in Marcy, Exploration of Red River . . . , 300. 1853.

Perennial with flat, linear leaf blades, the herbage mostly glabrous, infrequently the leaves puberulent. *Blades* with the lower margins usually sparsely ciliate

with pustular-based hairs. *Ligule* a short dense fringe of hairs seldom over 0.5 mm long. *Inflorescence* usually with 30–80 short pendulous branches; branches 1–3 (–4) cm long, bearing 1–12 or more spikelets, fewer at the culm apex than at the base. *Glumes* glabrous or scabrous, the first ⅔ or more as long as the second, the second usually 5.5–8 mm long. *Lemma* usually slightly shorter than the second glume, glabrous or scabrous-strigose, often minutely rugose, acute or slightly 3-toothed at the apex, with the nerves extending as a short mucro. *Palea* slightly shorter than the lemma and similar in texture. *Rudiment* variable but usually consisting of a lemma with a short membranous base and 3 unequally developed awns, the terminal awn occasionally as much as 7 mm long. *Caryopsis* narrowly ovate-elongate, 3.4–3.7 mm long, 6–7 times as long as broad.

1. Plants sod-forming or with the culms in small clumps, with creeping rhizomes, stolons or slender, trailing or decumbent culms.
   2. Stolons absent, the culms stiffly erect; creeping rhizomes present; anthers typically red or red orange; widespread in the U.S. ..... 14a. *B. curtipendula* var. *curtipendula*
   2′. Stolons present or the culms slender, decumbent and rooting at the lower nodes; creeping rhizomes present or absent; anthers usually yellow or red orange; northern and central Mexico ..... 14b. *B. curtipendula* var. *tenuis*
1′. Plants with stiffly erect culms in large or small clumps, stolons or creeping rhizomes not developed ..... 14c. *B. curtipendula* var. *caespitosa*

14a. **Bouteloua curtipendula** (Michaux) Torrey var. **curtipendula**—Fig. 14.

Chloris curtipendula Michaux, Fl. Bor. Am. 1: 59. 1803. TYPE: United States, Illinois, *Michaux* (US, holotype fragment). *Dineba curtipendula* (Michaux) Beauvois, Ess. Agrost. 98, 158, 160. 1812. *Eutriana curtipendula* (Michaux) Trinius, Fund. Agrost. 161. 1820. *Cynodon curtipendula* (Michaux) Raspail, Ann. Sci. Nat. (Paris) 5: 303. 1825. *Andropogon curtipendulum* (Michaux) Sprengel in Steudel, Nom. Bot., ed. 2, 1: 90. 1840. *Atheropogon curtipendulus* (Michaux) Fournier, Mex. Pl. Gram. 2: 138. 1886.

Atheropogon apludioides Muhl. in Willd., Sp. Pl. 4: 937. 1806. TYPE: "Habitat in America boreali." *Bouteloua melicaeformis* Roemer & Schultes, Syst. Veg. 2: 414. 1817, as synonym of *Atheropogon apludioides* Muhl. *Melica curtipendula* Michaux in Steudel, Nom. Bot. 1: 91, 519. 1821, as synonym of *Atheropogon apludioides* Muhl.

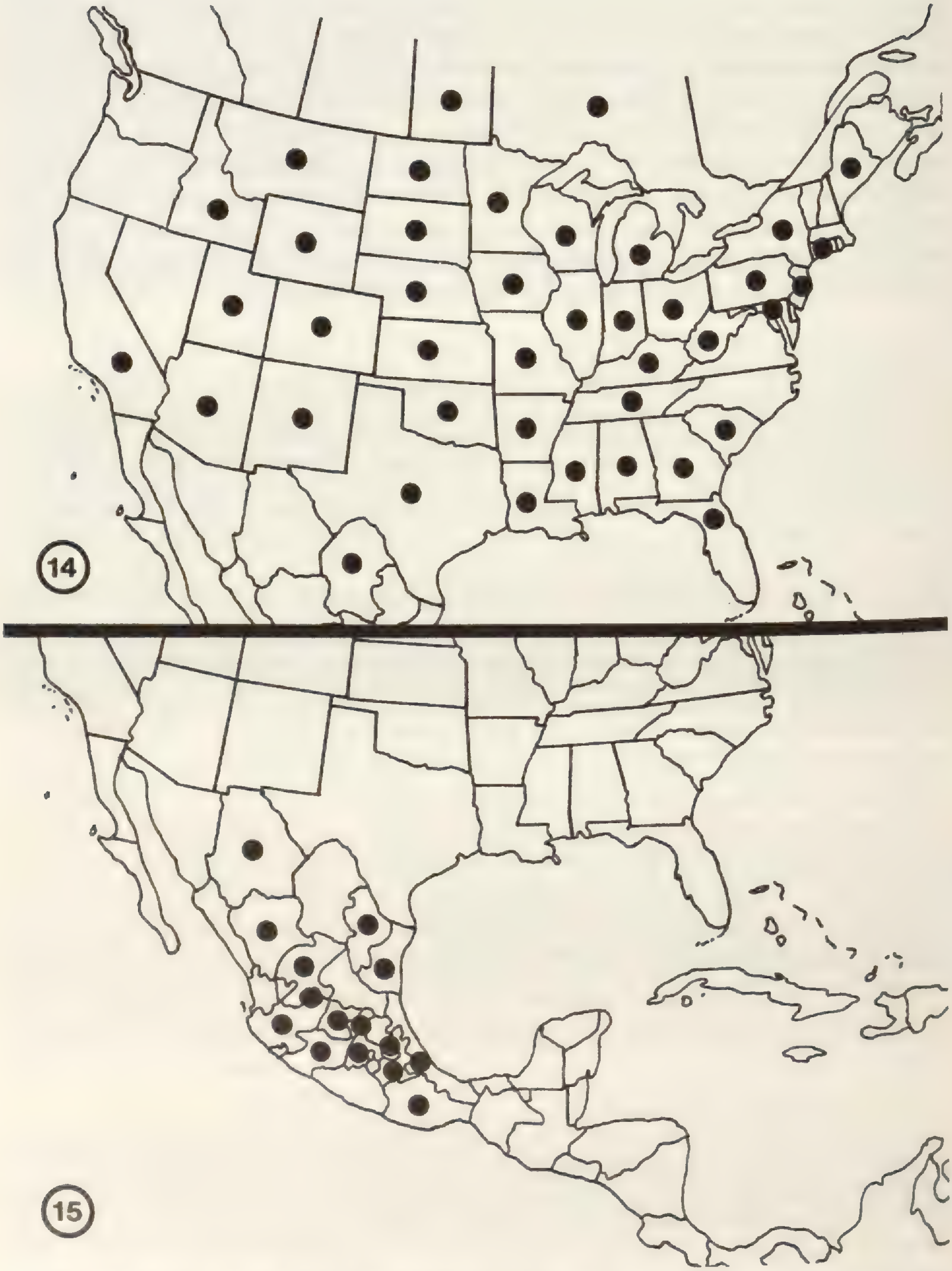
Cynosurus secundus Pursh, Fl. Amer. Sept. 728. 1814. TYPE: United States, "In upper Louisiana," *Bradbury*. *Dineba secunda* (Pursh) Roemer & Schultes, Syst. Veg. 2: 711. 1817. *Aristida secunda* Rud., in Roemer & Schultes, Syst. Veg. 2: 711. 1817, as synonym of *Dineba secunda* (Pursh) Roemer & Schultes.

Eutriana affinis Hooker f., Trans. Linn. Soc. London 20: 174. 1847. TYPES: "North America, *Schweinitz*, St. Louis, Missouri, and Texas, *Drummond*." *Heterostegon curtipendulus* Schwein. in Hook. f., Trans. Linn. Soc. London 20: 175. 1847, as synonym of *Eutriana affinis* Hooker f. *Atheropogon affinis* (Hooker f.) Fournier, Mex. Pl. Gram. 2: 141. 1886.

Bouteloua curtipendula (Michaux) Torrey var. *aristosa* A. Gray, Manual, ed. 2, 553. 1856. TYPE: United States, Illinois, *Geyer* (GH, isotype). *Bouteloua racemosa* Lag. var. *aristosa* (A. Gray) Watson & Coulter, in A. Gray, Manual, ed. 6, 656. 1890.

Culms single or in small clusters from slender or stout creeping rhizomes. *Blades* flat, usually 3–7 mm broad and bluish green but variable in width and color. *Inflorescence* typically large, with a stout axis bearing 40–70 or more reflexed branches, these with an average of 3–7 spikelets. *Glumes* and *lemmas* typically purple or purple-tinged. *Anthers* red or red orange, infrequently orange, yellow or purple.

HABITAT: A characteristic prairie grass, growing best on rich loamy, well-drained soils at elevations of from less than 100 m in southern Texas to over 2,500 m in the northwestern U.S.A.



FIGURES 14–15. Distribution of *Bouteloua* species.—14. *B. curtipendula* var. *curtipendula*. —15. *B. curtipendula* var. *tenuis*.

DISTRIBUTION: Widespread in North America from southeastern and south-central Canada (Ontario and Manitoba) through the prairie and plains regions of the central U.S.A. to eastern Montana and Colorado, southern Utah, Texas, New Mexico, Arizona and northcentral Mexico (Coahuila). There are scattered records in many states throughout the eastern U.S.A. from Maine to Florida.

Throughout most of its range, *B. curtipendula* var. *curtipendula* is regularly tetraploid ($2n = 40$) but in central and western Texas a high percentage of the plants are aneuploid with chromosome numbers from $2n = 41$ to $2n = 64$ (Gould & Kapadia, 1962a). Of interest is the recent report (Reeder, 1977) of a diploid, $2n = 20$ from South Dakota.

Following the authority of Hitchcock (1935), the name for this species is *Bouteloua curtipendula* (Michaux) Torrey, established in 1848 by Torrey. Recently, however, Dr. Robert A. Bye, Jr. (pers. comm.) noted that in the 1848 treatment, Torrey did not consider the plant at hand to be the same as *Chloris curtipendula* Michaux and did not properly transfer the species. Five years later, however, Torrey (1853) again published the name *Bouteloua curtipendula* and this time included *Chloris curtipendula* Michaux as a synonym.

14b. **Bouteloua curtipendula** (Michaux) Torrey var. **tenuis** Gould & Kapadia, Brittonia 16: 201. 1964. TYPE: Mexico, Zacatecas, 10 mi NW of Sombrerete, *Gould 9000* (TAES, holotype; TEX, UC, US, isotypes).—FIG. 15.

Culms slender, weak, in small tufts or clumps; stolons or stoloniferous culms usually developed, creeping rhizomes present or absent. *Leaf blades* moderately broad, relatively long and thin, the plants of western Mexico with conspicuously curled basal blades. *Inflorescence branches* with mostly 4–9 spikelets, these often rather widely spaced on the rachis. *Spikelet color* varying from brown or bronze to shades of purple. *Anthers* usually yellow or orange in plants of western Mexico and red or red orange in plants of eastern Mexico.

HABITAT: Open grasslands, mostly on loose, fertile soils at elevations from 100–2,500 m.

DISTRIBUTION: Widespread in Mexico south to the Isthmus of Tehuantepec, reported from the states of Aguascalientes, Chihuahua, Durango, Guanajuato, Jalisco, México, Michoacán, Nuevo León, Oaxaca, Puebla, Querétaro, Tamaulipas, Tlaxcala, Veracruz, and Zacatecas.

As stated by Gould & Kapadia (1964), two rather distinct "forms" of var. *tenuis* are distinguishable. Plants of eastern Mexico for the most part develop stolons but lack rhizomes, have straight basal blades, purple-tinged spikelets, and red or red orange anthers. Plants of western Mexico rarely develop stolons but often are rhizomatous. Characteristically they have conspicuously curled basal blades, brown or bronze-colored to purple spikelets, and yellow, orange, or orange yellow anthers. Only diploid ($2n = 20$) plants have been recorded from eastern Mexico whereas diploids, tetraploids, and aneuploid plants with $2n = 42$ are known from western Mexico. The type collection is diploid.

14c. **Bouteloua curtipendula** (Michaux) Torrey var. **caespitosa** Gould & Kapadia, Brittonia 16: 203. 1964. TYPE: United States, Arizona, Cochise

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FIGURE 16. Distribution of *Bouteloua curtipendula* var. *caespitosa*.

Co., 3 mi E of Bisbee at ca. 1,725 m elevation, *Gould 10021* (TAES, holotype; ARIZ, DS, GH, NY, TEX, UC, US, isotypes).—Fig. 16.

Bouteloua racemosa Lag., Varied. Ci. 2(4): 141. 1805. TYPE: Mexico. *Bouteloua pendula* Lag., Varied. Ci. 2(4): 141. 1805, as synonym of *B. racemosa*. *Atheropogon racemosus* (Lag.) Roemer & Schultes, Syst. Veg. 2: 414. 1817.

Atheropogon acuminatus Fournier, Mex. Pl. Gram. 2: 139. 1886. TYPES: Mexico, Mirador, *Liebmann* 583. Mexico, Potrero de Consquitla, *Liebmann* 584.

Culms caespitose, stiffly erect, 0.5–1.0 m tall, usually stout and in large clumps, often from a hard "knotty" base; stolons and creeping rhizomes not developed. *Leaf blades* variable in width and texture but most frequently narrow, thick and stiff, usually lacking the long, papilla-based hairs at the base that characteristically are present in the typical variety. *Inflorescence* highly variable, with few to numerous branches, with an average of 2–7 spikelets per branch. *Spikelet color* from bronze, yellowish brown or straw colored to green or various shades of purple. *Anthers* usually yellow or orange, infrequently red or purple.

HABITAT: Usually on loose, sandy or rocky, well-drained limey soils, at elevations from 200–2,500 m.

DISTRIBUTION: In North America, reported from southern Oklahoma, Colorado, Utah, and California south through the highlands of Mexico to Michoacán, Puebla and Chiapas. In South America, known from Venezuela, Bolivia, Uruguay, Peru, and Argentina.

Although most plants referrable to this taxon are believed to be apomictic, considerable morphological variation is exhibited between plants and populations in northern Mexico and the southwestern U.S.A. Relationships of this variety to other taxa of the "*B. curtipendula* complex" has been discussed by Gould & Kapadia (1962a, 1964) and Kapadia & Gould (1964b).

A few collections have been made of a striking "variant" of *B. curtipendula* var. *caespitosa* with stiffly erect rather than pendulous inflorescence branches. Garden seedings, however, have shown the erect inflorescence branch character to be highly unstable and not consistent even in seedlings grown from parent plants with erect inflorescence branches.

The collection *Rosengurtt B-4615* from Chipicuy, Paysandu, Uruguay, is of a plant with sprawling, many-noded culms but otherwise typical of *B. curtipendula* var. *caespitosa*. Two collections from Peru, *Jelski* 589 (TAES) from Callacate and *Ellenberg 1132* (MO) from west of Cusco are of exceedingly small plants, which may represent an unnamed taxon.

15. **Bouteloua repens** (H.B.K.) Scribner & Merrill, Bull. U.S.D.A. Div. Agrost. 24: 26. 1901.—Fig. 17.

Dineba repens H.B.K., Nov. Gen. Sp. Pl. 1: 172, *pl.* 52. 1816. TYPE: Mexico, Acapulco, *Humboldt & Bonpland*. *Atheropogon repens* (H.B.K.) Roemer & Schultes, Syst. Veg. 2: 416. 1817. *Eutriana repens* (H.B.K.) Trinius, Gram. Unifl. 241. 1824.

Heterosteca juncifolia Desvaux, Nouv. Bull. Sci. Soc. Philom. Paris 2: 188. 1810, not *Bouteloua juncifolia* Lag., 1816. TYPE: "Habitat in Antillis." *Eutriana heterostega* Trinius, Gram. Unifl. 242. 1824, based on "*Heterostega juncifolia* Desv. et Kunth." *Atheropogon juncifolius* (Desvaux) Sprengel, Syst. Veg. 1: 294. 1825. *Eutriana juncifolia* (Desvaux) Kunth, Rév. Gram. 1: 95. 1829. *Dineba juncifolia* (Desvaux) Steudel, Nom.

Bot., ed. 2, 1: 510. 1840. *Bouteloua heterostega* (Trinius) Griffiths, Contr. U.S. Natl. Herb. 14: 414, *fig.* 59. 1912.

Bouteloua bromoides Lag., Gen. & Sp. Nov. 5. 1816. TYPE: Mexico, Acapulco. *Actinochloa bromoides* (Lag.) Roemer & Schultes, Syst. Veg. 2: 420. 1817. *Eutriana bromoides* (Lag.) Trinius, Gram. Unifl. 241. 1824.

Atheropogon filiformis Fournier, Mex. Pl. Gram. 2: 140. 1886. TYPE: Mexico, "Hacienda de la Naranja," *Karwinski 991b*. *Bouteloua filiformis* (Fournier) Griffiths, Contr. U.S. Natl. Herb. 14: 413, *pl.* 82, 83. 1912.

Heterosteca rhadina Nash, Bull. Torrey Bot. Club 30: 386. 1903. TYPE: Puerto Rico, near Ponce, *Heller 6057*.

Bouteloua pubescens Pilger, Verh. Bot. Vereins Prov. Brandenburg 51: 193. 1909. TYPE: Guatemala, Dept. Huehuetenango, Malactan, *Seler 3224* (US, isotype).

Perennial. *Culms* erect or decumbent-spreading from a weak or firm and "knotty" base, mostly 20–50 cm tall. *Leaves* glabrous or sparsely hirsute, infrequently hirsute-hispid. *Ligule* a minute ciliate membrane. *Blades* linear, flat, 1–5 mm broad, ciliate with pustular-based hairs at least near the base. *Inflorescence* of 3–12 short, evenly spaced spikelet-bearing branches; branches bearing 3–9 (–20) imbricate spikelets, the branch deciduous with the spikelets at maturity. *Spikelets* 2-flowered, the lower floret perfect, the upper staminate or sterile, rarely perfect. *Rachilla* often extending as a short awn, glabrous, scabrous, or infrequently short-hispid on the nerve. *First glume* 4–7 mm long, the second slightly longer. *Lemma of the lower floret* 4.5–8 mm long, glabrous or infrequently bearded at the base, awnless or the nerves occasionally projecting as short awns. *Palea of the lower floret* narrow, often minutely 2-awned, usually slightly longer than the body of the lemma. *Upper floret* well developed, often broader than the lower. *Lemma of the upper floret* with a membranous body and 3 awns, the central awn stout and scabrous, mostly 4–8 (–10) mm long, the lateral awns more slender and slightly shorter, exserted well below the apex of the body of the lemma. *Anthers* mostly 3–4.5 mm long, usually orange or yellow, but occasionally red or purple. *Caryopsis* narrowly oblong, mostly 3–4 mm long; embryo ⅘ or more as long as the endosperm.

HABITAT: Open, usually hilly terrain, on a wide variety of soil types, present on sandy ocean shores near sea level to mountain slopes at elevations of 2,500 m or more.

DISTRIBUTION: Southern Texas (Bexar, Brooks, Dimmit, Hidalgo, Kennedy, Kleberg, and Webb counties), New Mexico (Catron and Hidalgo counties), Arizona (Cochise, Graham, Greenlee, Maricopa, Pima, Pinal, and Santa Cruz counties), and south through Mexico (27 states), the Antilles (Cuba, Dominican Republic, Haiti, Puerto Rico), and Central America to Colombia (Bolívar, Cauca, Tolima) and Venezuela (Aragua).

Gould (1969) recognized no subspecies or varieties in the species but delimited 9 "well defined forms" as follows: 1. Diploids ($2n = 20$) of the Antilles and the eastern coast of Mexico. 2. Diploids of southern Texas and adjacent Mexico. 3. Long-lived diploids and tetraploids ($2n = 40$) of the semi-arid regions of southern Arizona and northwestern Mexico. 4. Long-lived diploids and tetraploids of the mountains and foothills of eastern Mexico. 5. Tetraploids and hexaploids ($2n = 60$) of southcentral Mexico. 6. Coastal southern Mexico plants. 7.

Sinaloa form. 8. Plants of Central America and southern Mexico. 9. Plants of Venezuela and Colombia.

Diploids, for the most part, have slender, tufted culms from nonwoody, nonrhizomatous bases. Tetraploid and hexaploid plants tend to be larger and more robust than the diploids but are distinguished by no consistent morphological features.

Griffiths (1912) recognized five species in the *B. repens* "complex." He did not use the earliest published names *B. bromoides* Lag. or *B. juncifolia* Lag. as he considered them improperly used by Lagasca in *Bouteloua* and thus illegitimate. The five species listed by Griffiths were *B. americana*, *B. heterostega*, *B. filiformis*, *B. repens*, and *B. radicosa*. In the present treatment, *B. americana*, *B. repens*, and *B. radicosa* are retained as species, with populations referrable to *B. heterostega*, *B. filiformis*, and *B. repens* grouped under *B. repens*. *Bouteloua williamsii* Swallen, completes the series of four species in the complex.

A collection made near Chilpancingo, Guerrero, Mexico (*Hernández X-620060* [TAES]) is of a strong perennial plant with culms to 60 cm tall, and long, slender inflorescence branches to 4.5 cm long and with as many as 20 spikelets. The spikelets of the lower branches are widely spaced, often separated by rachis internodes 2–5 mm long.

16. **Bouteloua radicosa** (Fournier) Griffiths, Contr. U.S. Natl. Herb. 14: 411, *pl. 81*. 1912.—Fig. 18.

Dineba bromoides H.B.K., Nov. Gen. Sp. Pl. 1: 112, *pl. 51*. 1816, not *Bouteloua bromoides* Lag., 1816. TYPE: Mexico, "Crescit in temperatis scopulosis aridis inter Guanaxuato et Cubilete Mexicanorum," *Humboldt & Bonpland*.

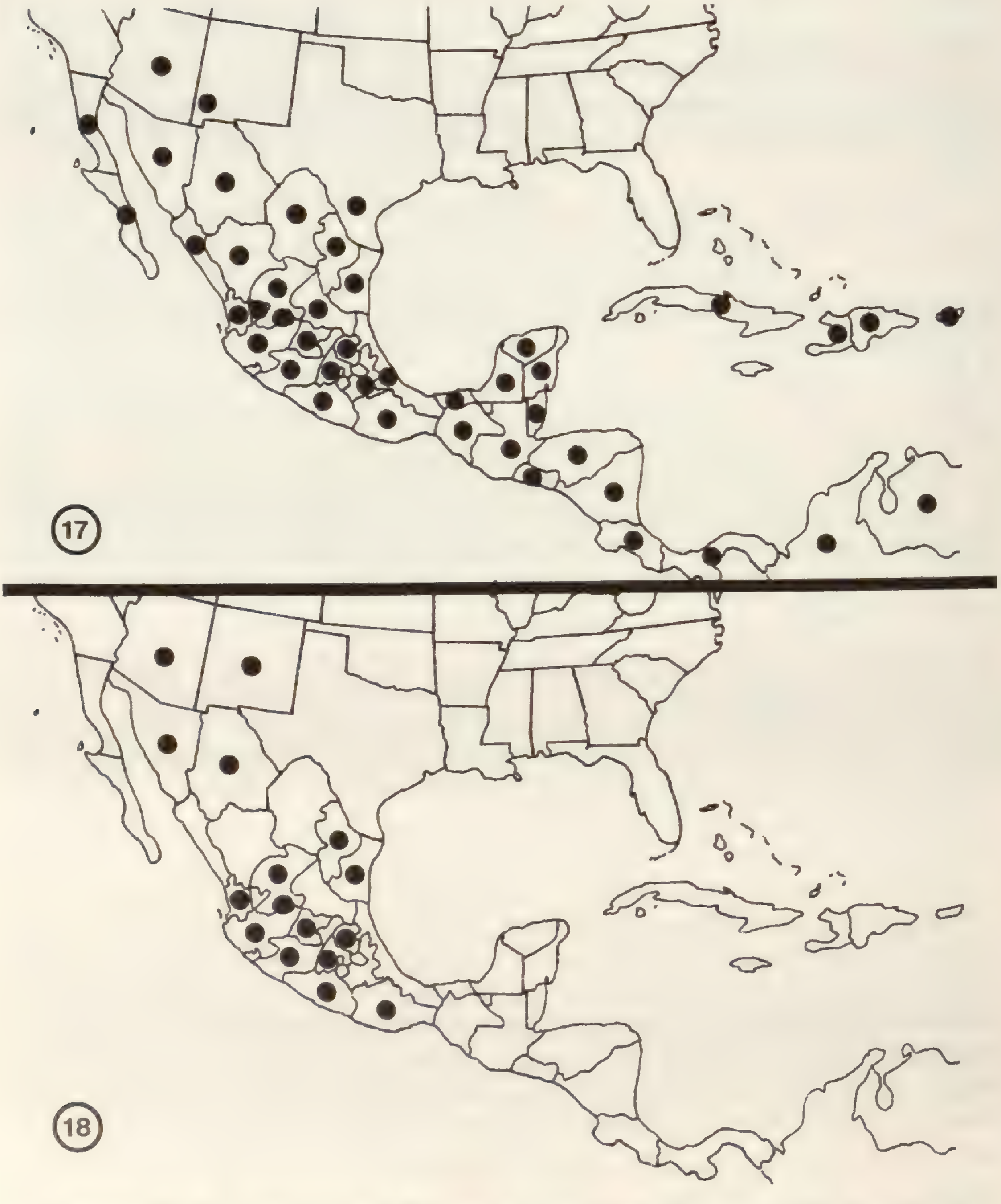
Atheropogon radicosus Fournier, Mex. Pl. Gram. 2: 140. 1886. TYPE: Mexico, vicinity of Mexico City, *Bourgeau 450* (F, GH, US, isotypes). *Bouteloua bromoides* Lag. var. *radicosa* (Fournier) Vasey ex L. H. Dewey, Contr. U.S. Natl. Herb. 2: 533. 1894.

Strong *perennial*. *Culms* from hard, stout rhizomatous bases, unbranched above the base, generally 40–80 cm tall but shorter in depauperate plants. *Rhizome* characteristically covered by firm, coarse, flattened, light-colored leaf sheaths. *Leaves* mostly in a basal cluster, the blades usually short and firm. *Inflorescence* highly variable as to length of branches, number of spikelets per branch, size of spikelet, and pubescence of the branch rachis, glumes, and lemmas. *Awns of the upper floret* well developed, the central one larger and longer than the lateral ones, projecting from a membranous, slightly bifid apex. *Caryopsis* not seen.

HABITAT: On dry, rocky slopes, at elevations of 1,000–3,000 m.

DISTRIBUTION: New Mexico (Catron, Grant, Hidalgo, and Socorro counties), Arizona (Apache, Cochise, Graham, Greenlee, Pima, Pinal, and Santa Cruz counties), and Mexico to Guerrero and Oaxaca (14 states).

As delimited by Gould (1969), *Bouteloua radicosa* is more restricted in its range than in the concept of Griffiths (1912). Striking variation in inflorescence characters exhibited by *B. radicosa* appears largely due to the influence of diploid and tetraploid forms of *B. repens* and of *B. williamsii*. Some populations have large bristly spikelets borne on short inflorescence branches, large florets, with



Figures 17–18. Distribution of *Bouteloua* species.—17. *B. repens*.—18. *B. radicosa*.

the lemma of the lower floret glabrous and awnless or nearly so, and the upper floret staminate or perfect. These are charcters of *B. repens*. As has been noted in the discussion of *B. williamsii*, numerous plants of *B. radicosa* exhibit the following characteristics of the species: long inflorescence branches with many small spikelets; lemma of the lower floret relatively small, with a tuft of hairs at the base and with well-developed lateral, as well as terminal, awns; palea strigose-pubescent; upper floret neuter and with a narrow, short-awned lemma.

Populations referrable to *B. radicosa* probably should be viewed as a series

of dryland ecotypes developed from diploids and possibly tetraploids of the basic *B. repens* stock, with the strong influence of the tropical *B. williamsii* evident throughout much of the range. Some plants of *B. repens* have hard, knotty, rhizomatous culm bases that approach the condition in *B. radicosa*. Rhizomatous plants from Tamaulipas and Nuevo León are of this form.

17. **Bouteloua alamosana** Vasey, Contr. U.S. Natl. Herb. 1: 115. 1891. TYPE: Mexico, Sonora, Alamos, *Palmer* 698, September 1890 (US, holotype; NY, TAES, isotypes).—FIG. 19.

Bouteloua longiseta Gould, Brittonia 21: 271. 1969. TYPE: Mexico, Chiapas, 9 km SW of Cintalapa, *Gould 12759* (TAES, holotype; GH, isotype).

Tufted *annual*. *Culms* erect or spreading-erect, often much-branched, 15–40 cm tall, the closely grazed or otherwise stunted plants with flowering culms 8 cm tall or less. *Sheaths* and both leaf surfaces sparsely to densely hispid, some or all of the hairs with pustulate bases. *Inflorescence* with (3–) 4–8 branches, the main axis 3–10 cm long above the basal branch; branches bearing 3–8 spikelets, the rachis usually densely strigose-hirsute at least on the angles of the lower portion, and with a tuft of hair below each spikelet. *Glumes* 6–9 mm long, acuminate or short awn-tipped, usually strigose-pubescent on the nerves but occasionally only scabrous. *Lemma* of the lower floret glabrous, 3-awned, the awns 1–2 mm long. *Palea* of the lower floret about as long as the lemma, with strong, greenish nerves that project above as short awns. *Upper floret* with 3 nearly equally developed, usually scabrous awns (8–) 11–14 mm long. *Caryopsis* narrowly obovate, 4–4.5 mm long.

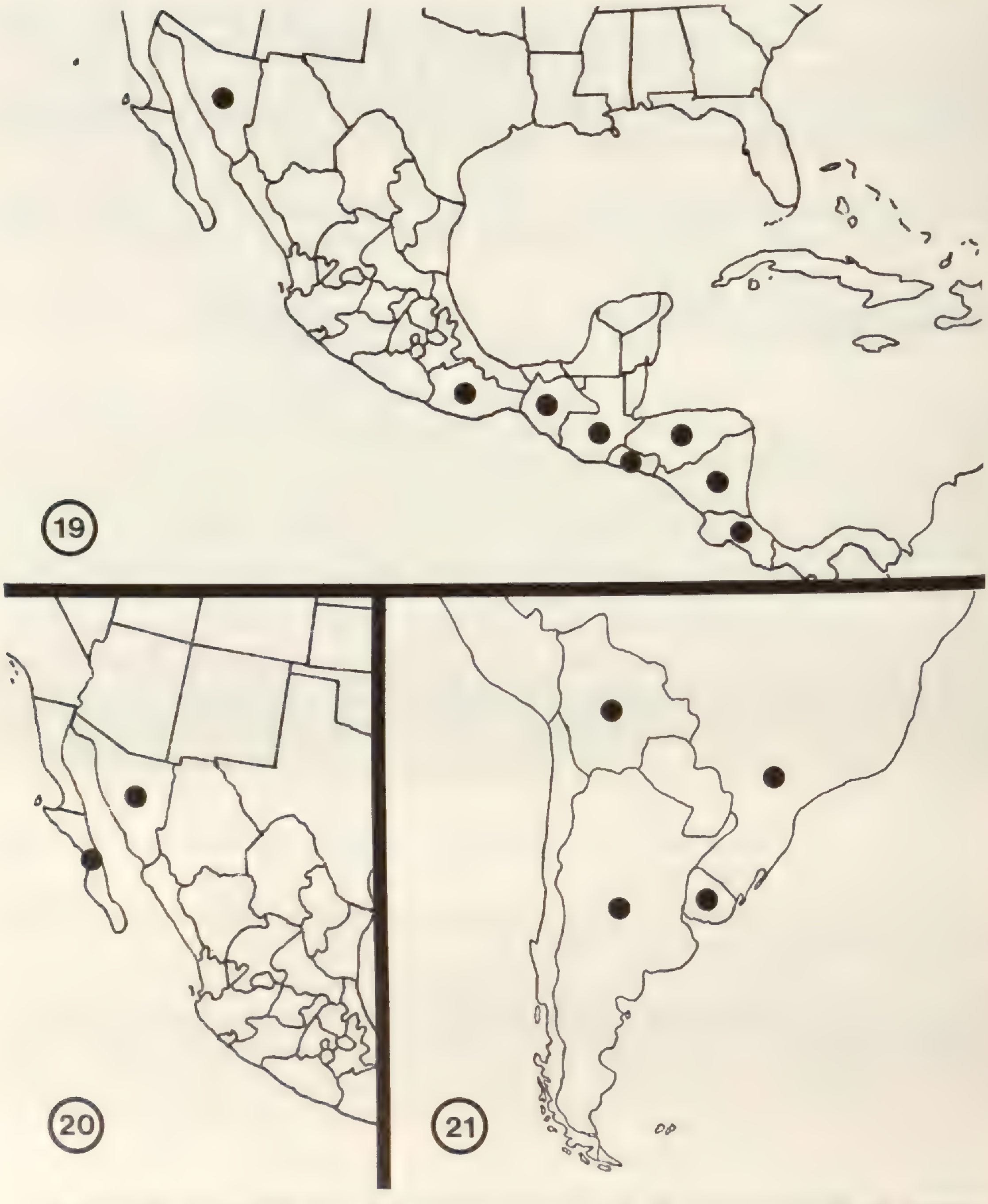
HABITAT: On open, clayey or sandy soils, at elevations from less than 100 m (at Alamos) to about 2,000 m.

DISTRIBUTION: Mexico (Chiapas, Oaxaca, Sonora), Guatemala, El Salvador, Honduras, Nicaragua, and Costa Rica.

In the mountains south of Oaxaca, Mexico, on hard packed gravelly soil of a road shoulder, *B. alamosana* was observed to form a dense sod similar in general aspect to *Cynodon dactylon*. In western Chiapas it was associated with the annual *Aristida adscensionis* in loose soil along a roadside ditch. Of special interest is the observation by Gould (1969) that anthers of *B. alamosana* collected in southern Mexico were only about 1 mm long on all specimens with measurable anthers. This contrasts sharply with the usual anther length of 3–4.5 mm in the closely related *B. repens*.

18. **Bouteloua annua** Swallen, J. Wash. Acad. Sci. 25: 414. 1935. TYPE: Mexico, Baja California Sur, 4 mi E of San Ignacio, *Forrest Shreve 7032* (US, holotype; GH, US, isotypes).—FIG. 20.

Tufted *annual*. *Culms* slender, geniculate-erect, mostly 10–25 cm long, branching at the lower and middle nodes to produce short, lateral inflorescence-bearing branches. *Sheaths* glabrous or with papilla-based hairs present on the upper portion of the sheath margins. *Ligule* ciliate, 0.2 mm long. *Blades* short and flat,



FIGURES 19–21. Distribution of *Bouteloua* species.—19. *B. alamosana*.—20. *B. annua*.—21. *B. megapotamica*.

mostly 2–4 cm long and 1.5–3 mm broad, glabrous or somewhat pubescent on the upper surface and ciliate on the margins below the middle. *Inflorescence of main culms* usually with 3–7 spicate branches, those of the short lateral culms often with 1–2 branches; branches mostly 2.5–3 cm long, with 4–7 spikelets, the rachis glabrous or minutely scabrous. *Glumes* glabrous or minutely scabrous on the midnerve, acute or acuminate, occasionally with a short, stout awn. *First glume* narrow, 3.5–4 mm long, the second glume much broader, 6–8 mm long. *Lemma of the*

lower floret 7–9 mm long, densely pubescent at the base, sparsely scabrous-hirsute above, the 3 nerves extending into short awns or teeth at the tip. *Upper floret* with the lemma reduced to a hirsute, terete awn column bearing 3 flattened, scabrous awns mostly 5–8 mm long, the palea absent. *Caryopsis* not seen.

HABITAT: On dry, rocky, open slopes at low elevations.

DISTRIBUTION: Known only from three Mexican collections, two from Baja California Sur (*Shreve 7032* [TAES] from the San Ignacio location, *Jones 24070* [TAES] from La Paz), and *Wiggins 7941* (TAES) from near Santa Rosalia, Sonora.

Bouteloua annua is similar to forms of *B. repens* and *B. alamosana* in inflorescence characters but differs from both in the greatly reduced upper floret (rudiment) which has no palea. From *B. repens* it also differs in the annual habit, and from *B. alamosana* it can be distinguished by the nonhirsute lower portion of the inflorescence branch.

19. **Bouteloua megapotamica** (Sprengel) Kuntze, Rev. Gen. Pl. 3(3): 341. 1898.—FIG. 21.

Pappophorum megapotamicum Sprengel, Syst. Veg. 4: Cur. Post, 34. 1824. TYPE: Brazil, "Rio Grande," *Sello*.

Eutriana multiseta Nees, Agrost. Bras. 413. 1829. TYPE: Uruguay, Montevideo, *Sello* (B, holotype, examined by Griffiths). *Pappophorum eutrianoides* Trinius in Nees, Agrost. Bras. 414. 1829, as a synonym of *Eutriana multiseta* Nees. *Bouteloua multiseta* (Nees) Grisebach, Abh. Königl. Ges. Wiss. Göttingen 19: 303. 1879.

Tufted, strongly stoloniferous *perennial*. *Culms* curving-erect, mostly 15–25 cm tall. *Leaves* clustered on the lower part of the culm. *Ligule* a fringe of long hairs. *Blades* sparsely hairy, firm, narrow, acuminate at the apex, 10 cm long. *Inflorescence* branches mostly 2–6, bearing 3–10 bristly spikelets closely placed on a short hairy, flattened rachis, this extended into 2 equal or unequal awns. *Glumes* 1-nerved, the first narrow, reduced, setaceous or tapering to a slender awn tip, the second large and broad, with a stout scaberulous midnerve and irregularly 1–3 awned at the apex. *Lemma of the lower floret* (including awns) mostly 9–12 mm long, smooth, shiny, with a short, stout terminal awn and 2 lateral awns, the terminal awn usually with 2 slender setae at the base. *Palea* 8–9 mm long, 2-awned. *Rudiments* densely clustered, usually 2–3, these reduced to 3 awns 2–3 cm long, with usually 2 slender elongated setaceous membranes at the base. *Caryopsis* cylindrical-obovate, 2–2.5 mm long; embryo ¾ or more as long as the endosperm.

HABITAT: Most commonly on heavy (clayey) soils but occasionally in sand, at elevations from near sea level to 2,500 m.

DISTRIBUTION: Southern Brazil, Bolivia, Argentina, and Uruguay.

This is the only species of *Bouteloua* that does not occur in North America.

20. **Bouteloua rigidiseta** (Steudel) Hitchcock, J. Wash. Acad. Sci. 23: 453. 1933.—FIG. 22.

Aegopogon rigidisetus Steudel, Syn. Pl. Glum. 146. 1854. TYPE: United States, Texas, *Drummond* (US, holotype fragment).

Bouteloua texana S. Watson, Proc. Amer. Acad. Arts 18: 196. 1883. TYPE: United States, Texas, San Antonio de Bejar, *Berlandier 1535* (GH, isotype). *Polydon texanus* (S. Watson) Nash in Small, Fl. SE. U.S. 138, 1327. 1903.

Tufted *perennial*. *Culms* slender, weak, (10–) 15–40 (–50) cm tall, densely clustered in usually small clumps. *Ligule* a minute fringe of short hairs. *Blades* narrow, flat or somewhat involute, mostly 4–12 (–17) cm long and 1–2 mm broad, usually sparsely pilose. *Inflorescence axis* mostly 3–6 cm long above the lowermost branch; inflorescence branches with their spikelets short, wedge shaped, mostly 0.8–1.6 mm long including the awns, with (2–) 3–5 closely placed, spreading spikelets; the branch rachis sparsely hispid above the hairy base, mostly 4–7 mm long, deeply forked or trifurcate at the apex, disarticulating ca. 0.5 mm above the base, leaving a persistent, short stub on the main axis. *Spikelet* with one fertile floret and one greatly reduced floret. *Glumes* unequal, the second large, sparsely appressed-pubescent, with a stout midnerve that continues into a short, stout awn from between 2 thin, narrow, pointed apical lobes. *Lemma of the lower floret* with a glabrous or sparsely hairy body mostly 2.5–4 mm long, this divided above into 2 stout, short, spreading lateral awns and a slightly longer terminal awn from between the teeth of a notched apex. *Upper floret* rudimentary, usually reduced to an awn column and 3 awns 5–10 mm long. *Caryopsis* narrowly obovate, flattened, 3.5–3.7 mm long; embryo ca. ⅔ as long as the endosperm.

HABITAT: Grassy pastures and woods openings, most commonly in clay or sandy-clay soils, at elevations of from near sea level to about 700 m.

DISTRIBUTION: Oklahoma (Carter, Cleveland, Comanche, Marshall, and Swanson counties), 51 counties in central and southern Texas, and northeastern Mexico (Coahuila and Tamaulipas).

Commonly called "Texas grama," this shallow-rooted, short-lived perennial is among the first of the warm-season grasses to flower in the spring. Although widespread and abundant in Texas in heavily pastured areas, this grass has little value as a forage plant.

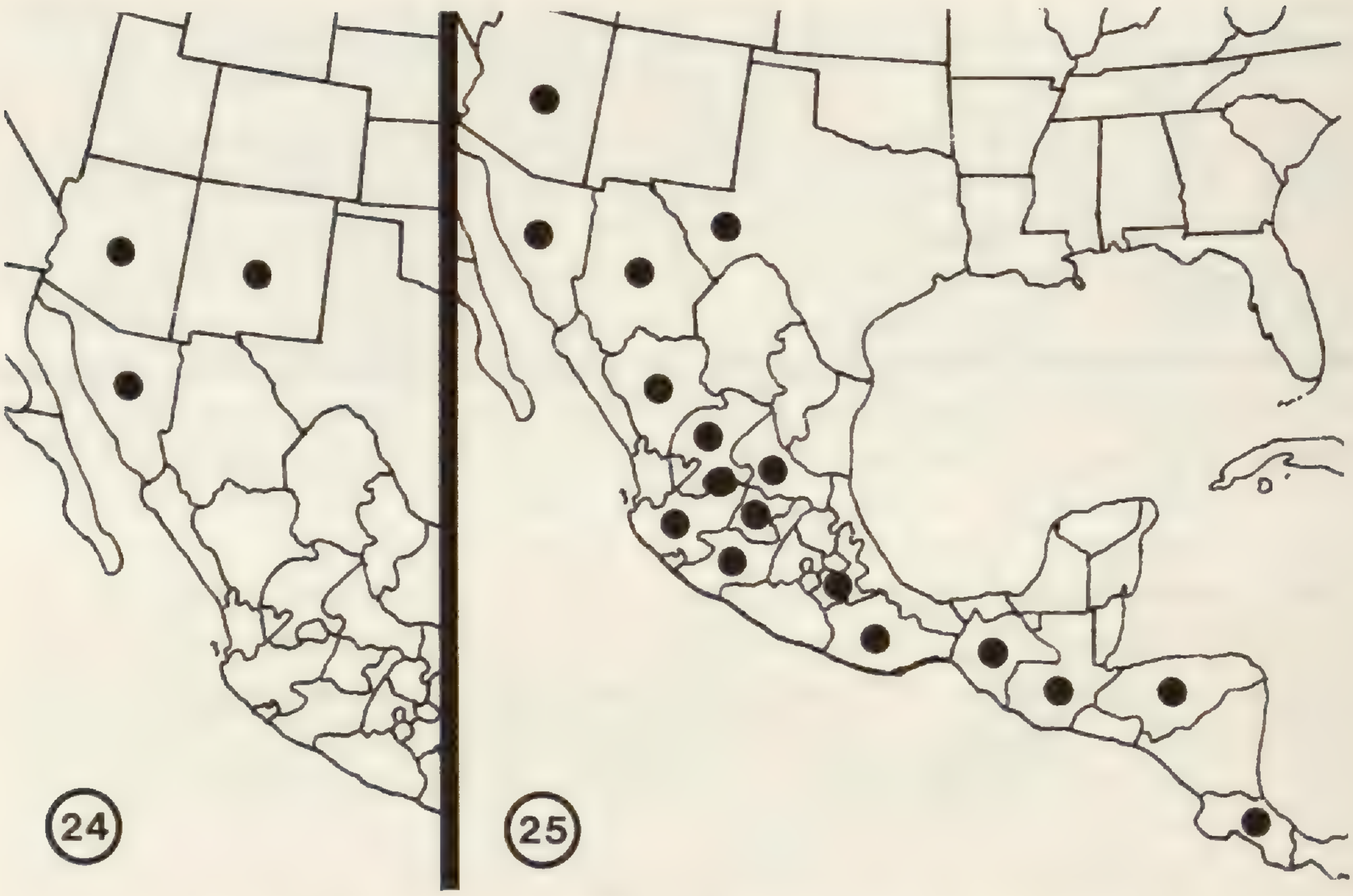
21. **Bouteloua aristidoides** (H.B.K.) Grisebach, Fl. Brit. W. I. 537. 1864.

Tufted, short-lived *annual*. *Culms* weak, slender, 6–50 cm or more long, the lateral culms of a tuft geniculate and curving-erect from a decumbent base. *Sheaths* usually much shorter than the internodes. *Ligule* a fringe of short hairs. *Blades* short, thin, flat or folded, 1–2 mm broad, often with a few long stiff hairs at the base and occasionally extending up the adaxial surface. *Inflorescence* mostly 2.5–10 cm long, usually with 4–15 short, loosely spaced and spreading, readily deciduous branches; branch rachis flattened, densely pubescent at least near the base, the curved tip extended 5–10 mm beyond the insertion of the terminal spikelet. *Lowermost spikelet* of the branch closely appressed to the rachis, usually without a rudiment and with an awnless or minutely awned lemma. *Upper spikelets* of the branch, with a rudiment reduced to an awn column and 3 awns 2–6 mm long. *Glumes* very unequal, narrowly acute or acuminate, the large upper one often spreading at a wide angle from the floret. *Lemma* about as long as the upper

FIGURES 22–23. Distribution of *Bouteloua* species.—22. *B. rigidiseta*.—23. *B. aristidoides* var. *aristidoides*.

glume, with short or long awns. *Caryopsis* brownish, narrow, flattened, mostly 2.5–3 mm long.

1. Spicate branches with 2–5 spikelets, mostly 1.6 cm or less long to the tip of the terminal spikelet; rachis usually extended 6–10 mm or more beyond the point of attachment of the terminal spikelet ..... 21a. *B. aristidoides* var. *aristidoides*



Figures 24–25. Distribution of *Bouteloua* species.—24. *B. aristidoides* var. *arizonica*. —25. *B. chondroisioides*.

1′. Spicate branches with 6–10 spikelets, mostly 1.5–3.5 cm long; rachis extended 2–5(–7) mm beyond the point of attachment of the terminal spikelet ---------- 21b. *B. aristidoides* var. *arizonica*

21a. **Bouteloua aristidoides** (H.B.K.) Grisebach var. **aristidoides**.—Fig. 23.

Dineba aristidoides H.B.K., Nov. Gen. Sp. Pl. 1: 171. 1816. TYPE: Mexico, *Humboldt & Bonpland* (P, holotype). *Atheropogon aristidoides* (H.B.K.) Roemer & Schultes, Syst. Veg. 2: 415. 1817. *Eutriana aristidoides* (H.B.K.) Trinius, Gram. Unifl. 242. 1824. *Aristida unilateralis* Willd. ex Steudel, Nom. Bot., ed. 2, 1: 132. 1840, as synonym of *Eutriana aristidoides* Trinius. *Triathera aristidoides* Nash in Small, Fl. SE. U.S. 137. 1903.

Dineba hirsuta Presl, Rel. Haenk. 1: 292. 1830. TYPE: Peru, *Haenke*. *Eutriana hirsuta* (Presl) Kunth, Enum. Pl. 1: 280. 1833.

Bouteloua ciliata Grisebach, Abh. Königl. Ges. Wiss. Göttingen 24: 302. 1870. TYPE: Argentina, Juramento, *Lorentz & Hieronymus* 352 (US, holotype fragment).

Bouteloua gracilis Vasey in Wheeler, Rep. U.S. Survey 100th Merid. 6: 287. 1878, not *Bouteloua gracilis* Lag., 1840. TYPE: United States, Arizona, "Riley's Well," *Rothrock 701* (US, holotype).

Habitat: Dry mesas, plains, and washes, from near sea level to about 2,000 m elevation. A "six weeks grass" which frequently is abundant over large areas following summer showers.

Distribution: Western Texas to California and south through Mexico to Oaxaca; on the island of Aruba and with a few records from Bolivia, Brazil, Columbia, Ecuador, Paraguay, Peru; frequent in Argentina (provinces of Catamarca, Córdoba, La Rioja, Mendoza, Salta, San Juan, San Luia, Santiago del Estero, and Tucumán).

The general record in North America is as follows: Texas (Brewster, Burnet,

Culberson, Dimmit, Edwards, El Paso, Hidalgo, Hudspeth, Jeff Davis, Llano, Mason, Maverick, Presidio, Val Verde, and Webb counties). New Mexico (Dona Ana, Grant, and Hidalgo counties). Arizona (all counties except Apache Navajo). Nevada (Clark and Lincoln counties). California (Riverside, San Bernardino, and San Diego counties). Mexico (states of Aguascalientes, Baja California, Baja California Sur, Chihuahua, Coahuila, Colima, Durango, Jalisco, Nuevo León, Nayarit, Oaxaca, San Luis Potosí, Querétaro, Sinaloa, Sonora, and Zacatecas).

21b. **Bouteloua aristidoides** (H.B.K.) Grisebach var. **arizonica** M. E. Jones, Contr. W. Bot. 14: 13. 1912. TYPE: United States, Arizona, Pima Co., Tucson, Thornber 177 (US, holotype fragment).—FIG. 24.

HABITAT: In the same dry, exposed sites as *B. aristidoides* var. *aristidoides*, at elevations of 500–800 m.

DISTRIBUTION: New Mexico (between Lordsburg and Deming, Hidalgo or Luna counties), Arizona (Pima, Pinal, and Santa Cruz counties), and northern Mexico (Sonora, 25 mi W of Angostura).

In its extreme form var. *arizonica* differs strikingly from var. *aristidoides* but the two varieties intergrade freely.

22. **Bouteloua chondrosioides** (H.B.K.) Bentham ex S. Watson, Proc. Amer. Acad. Arts 18: 179. 1883.—FIG. 25.

Dineba chondrosioides H.B.K., Nov. Gen. Sp. Pl. 1: 173, *tab.* 53. 1816. TYPE: Mexico, *Humboldt & Bonpland* (P, holotype). *Atheropogon chondrosioides* (H.B.K.) Roemer & Schultes, Syst. Veg. 2: 416. 1817. *Eutriana cristata* Trinius, Gram. Unifl. 241. 1824, based on *Atheropogon chondrosioides* Roemer & Schultes. *Chondrosium humboldtianum* Kunth, Rév. Gram. 1: 93. 1829, based on *Dineba chondrosioides* H.B.K.

Bouteloua ovata Lag., Gen. & Sp. Nov. 5. 1816. TYPE: Mexico. *Actinochloa ovata* (Lag.) Roemer & Schultes, Syst. Veg. 2: 420. 1817.

Bouteloua havardii Vasey ex S. Watson, Proc. Amer. Acad. Arts 18: 179. 1883. TYPE: United States, Texas, Limpio Mts., *Havard* 53 in 1881 (US, holotype; GH, isotype).

Tufted *perennial* with erect culms from a firm but not rhizomatous base. *Culms* mostly 30–60 cm tall. *Sheaths* often with a few long hairs on the upper margins. *Ligule* a minute, fringe of hairs. *Blades* short, flat, glaucous, 1–2.5 mm broad, usually ciliate on the lower margins with long, papilla-based hairs and often with a few hairs on either or both surfaces. *Infloresecence* axis 2.5–6 cm long above the lowermost branch, with 3–8 (–10) short, densely flowered branches mostly 1–15 cm long excluding the awns, the branch rachis 6–15 mm long, densely pubescent, the tip extended as a point well beyond the insertion of the uppermost spikelet. *Spikelets* closely placed, mostly 8–12 per branch, with one fertile floret and a single, awned rudiment above; all exposed spikelet structures more or less hairy. *First glume* ca. 3 mm long, the second ca. 4 mm long. *Lemma of the lower floret* shallowly 3-cleft, the divisions muticous or short-awned. *Lemma of the rudimentary upper floret* 3-awned, the body cleft nearly to the base or reduced to a slender awn column. *Anthers* 3.5–4 mm long. *Caryopsis* narrowly oval, ca. 2.5 mm long and 0.9 mm broad.

HABITAT. Dry open slopes at elevations of 200–2,500 m.

DISTRIBUTION: Western Texas (Brewster, Erath, Jeff Davis, and Presidio counties), Arizona (Cochise, Pima, and Santa Cruz counties), Mexico (states of Aguascalientes, Chiapas, Chihuahua, Durango, Guanajuato, Jalisco, Michoacán, Oaxaca, Puebla, San Luis Potosí, Sonora, and Zacatecas), Guatemala, Honduras, and Costa Rica.

Bouteloua chondrosioides is one of the better range forage species adapted to dry grassland areas.

23. **Bouteloua eludens** Griffiths, Contr. U.S. Natl. Herb. 14: 401. 1912. TYPE: United States, Arizona, Pima Co., Santa Rita Mts., *David Griffiths 7269* (US, holotype; GH, isotype).—FIG. 26.

Perennial. Culms slender, mostly 35–60 cm tall from a firm leafy base. *Basal sheaths* tightly packed, somewhat papery, usually light straw-colored. *Sheaths* glabrous or with a few hairs on the margins near the apex. *Ligule* a short lacerate membrane. *Blades* flat and narrow, mostly 1–3 mm broad, the upper blades glabrous, the lower ones often variously hispid or scabrous. *Inflorescence* mostly 7–10 cm long, usually with 10–20 readily deciduous branches, these mostly 7–11 mm long, including the awns, and with 3–5 spikelets. Glumes acute, acuminate or short-awned, silvery-hispid. *Lemma of the lower floret* hispid, the lateral nerves extended as acuminate, flattened lobes 0.5–2 mm long, the apex with a flattened, acuminate or setaceous tip of about the same length as the lateral lobes. *Rudimentary floret* one, usually with a well-developed hispid body, the 2 lateral nerves extended into flattened hispid lobes or awns 0.5–3 (–4) mm long, the medial nerve forming a flattened hispid-scabrous awn mostly 1–3 (–5) mm long from between 2 slender, setaceous lobes. *Caryopsis* obovate, about 5 mm long and 1.5 mm mm broad.

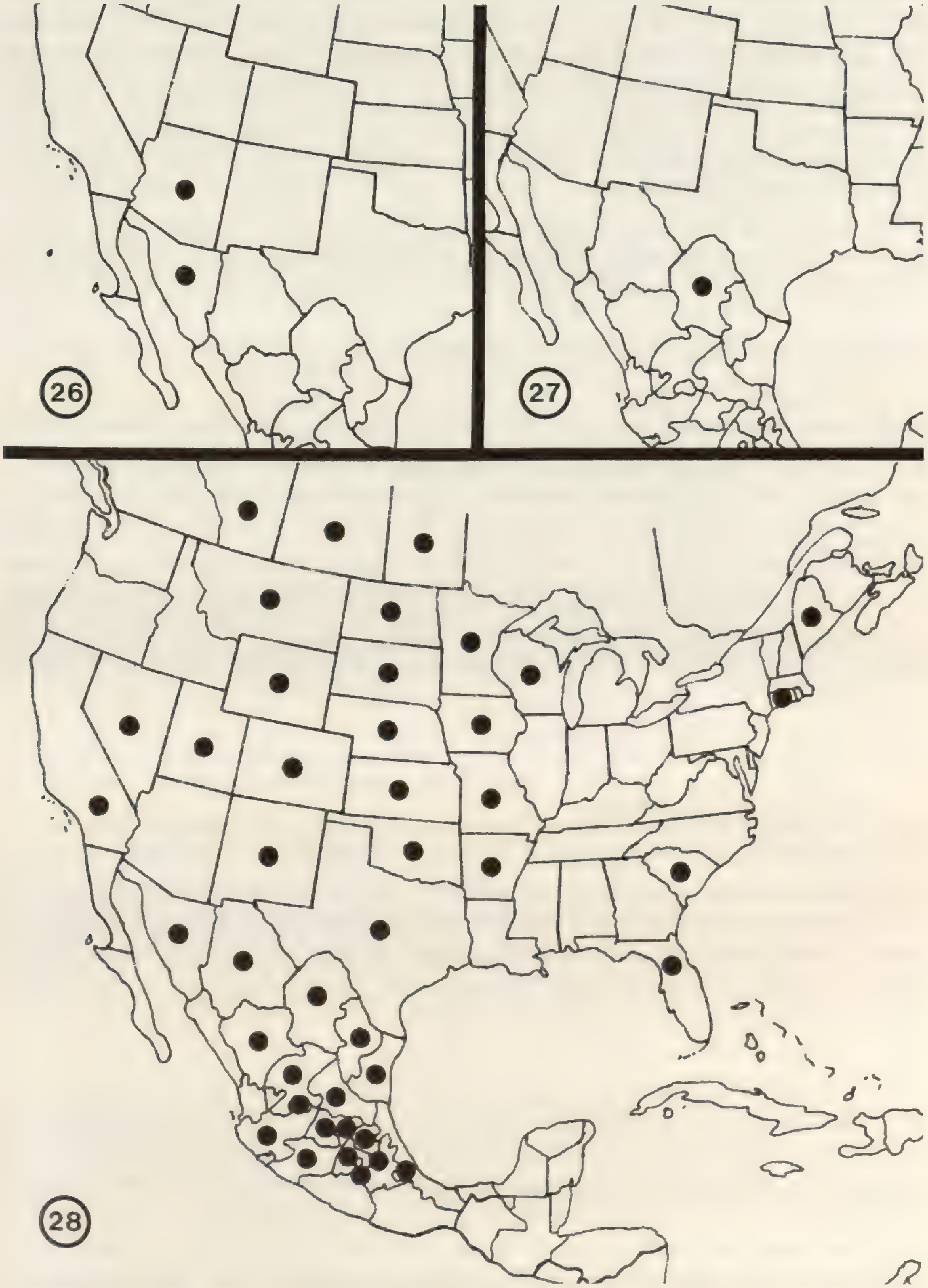
HABITAT: On dry, rocky slopes and rolling desert flats, mostly at 1,200–1,800 m elevation.

DISTRIBUTION: Southern Arizona (Cochise, Pima, and Santa Cruz counties) and northern Sonora, Mexico.

Bouteloua eludens is a relatively rare species, known only from a few localities in the area of distribution. It appears closely related to the more widespread *B. chondrosioides*.

24. **Bouteloua johnstonii** Swallen, Proc. Biol. Soc. Wash. 56: 79. 1943. TYPE: Mexico, Coahuila, South end of Canada Oscuro near Tanque La Luz, *I. M. Johnston 8491* (NA, holotype; GH, US, isotypes).—FIG. 27.

Culms densely tufted, 10–30 cm tall, from hard, rhizomatous, much-branched bases. *Blades* stiff, narrow, recurved-spreading, involute with stiff spinose tips. *Inflorescence* long exserted, with 6–12 deciduous branches; branches mostly 8–15 mm long, bearing 7–11 spikelets. *Spikelets* with 1–2 rudimentary florets above the perfect one. *Glumes* thin, acute to acuminate or short-awned, the first glabrous, mostly ½ or less as long as the second, the second sparsely hirsute, 5–7 mm long. *Lemma of the lower floret* glabrous, the lateral nerves excurrent as short, scabrous



FIGURES 26–28. Distribution of *Bouteloua* species.—26. *B. eludens*.—27. *B. johnstonii*.—28. *B. gracilis*.

awns, the midnerve continued as a stout scabrous awn 2–3 mm long between 2 membranous setaceous lobes. *Upper floret* or *florets* rudimentary, the larger (lower) one reduced to a glabrous terete awn column with 3 scabrous awns mostly 2–3 mm long and 4 setaceous shorter awns or awn-tipped lobes. *Caryopsis* not seen.

HABITAT: Gypsum beds.

DISTRIBUTION: A rare species of western Coahuila, Mexico, known only from the type and one other collection, *I. Johnston 8751* (US), from "SW end of Canada Oscuro near Tanque La Luz."

In describing the species Swallen (1943) noted that it is distinguished from the closely related *B. chondrosioides* and *B. eludens* by the firm, involute, recurved-spreading blades and the glabrous or inconspicuously hairy second glumes.

25. **Bouteloua gracilis** (H.B.K.) Griffiths, Contr. U.S. Natl. Herb. 44: 375. 1912.—FIG. 28.

Chondrosium gracile H.B.K., Nov. Gen. Sp. Pl. 1: 176, *tab.* 58. 1816. TYPE: Mexico, "Crescit in crepidinibus et devexis montis porphyritici La Buffa de Guanaxuato Mexicanorum" *Humboldt & Bonpland. Actinochloa gracilis* (H.B.K.) Willd. ex Roemer & Schultes, Syst. Veg. 2: 418. 1817. *Eutriana gracilis* (H.B.K.) Trinius, Gram. Unifl. 240. 1824, based on *Actinochloa gracilis* Willd. ex Roemer & Schultes. *Atheropogon gracilis* (H.B.K.) Sprengel, Syst. Veg. 1: 293. 1825.

Atheropogon oligostachyus Nuttall, Gen. Pl. 1: 78. 1818. TYPE: United States, plains of the upper Missouri, *Nuttall. Eutriana oligostachya* (Nuttall) Kunth, Rév. Gram. 1: 96. 1829. *Chondrosium oligostachyum* (Nuttall) Torrey, in Marcy, Expl. Red River. 300. 1852. *Bouteloua oligostachya* (Nuttall) Torrey ex A. Gray, Manual, ed. 2, 553. 1856.

Chondrosium gracile H.B.K. var. *polystachyum* Nees, Linnaea 19: 692. 1847. TYPE: Mexico, *Aschenborn 153.*

Bouteloua stricta Vasey, Bull. Torrey Bot. Club 15: 49. 1888. TYPE: United States, Texas, *G. C. Nealley* in 1887 (US, holotype).

Bouteloua oligostachya (Nuttall) Torrey ex A. Gray var. *major* Vasey ex L. H. Dewey, Contr. U.S. Natl. Herb. 2: 531. 1894. TYPE: United States, Arizona, without locality, *J. G. Lemmon 427* (US, holotype).

Bouteloua oligostachya (Nuttall) Torrey ex A. Gray var. *pallida* Scribner ex Beal, Grasses N. Amer. 2: 418. 1896. TYPE: Mexico, 23 Aug. 1885, *Pringle 407* (US, isotype).

Tufted *perennial*, frequently with short, stout rhizomes. *Culms* mostly 25–60 (–70) cm long but occasionally much shorter, erect or somewhat geniculate at the base; nodes glabrous or minutely puberulent. *Sheaths* glabrous or sparsely long-hirsute. *Ligule* a fringe of short hairs, often with marginal tufts of long hairs. *Blades* short, flat at the base, 1–2.5 mm broad, usually scabrous or short-pubescent on the axial surface and often sparsely hirsute. *Inflorescence* with 1–3(–4) branches; branches 1.5–5(–7) cm long, thick and densely flowered; the rachis scabrous on the back, terminated at the apex by a spikelet, this usually reduced and often appearing as a continuation of the rachis. *Spikelets* commonly 40–90 or more per branch, closely placed and pectinately spreading. *Glumes* glabrous or scabrous to hirsute on the midnerve with papilla-based hairs. *Lemmas* mostly 4–5.5 mm long, pubescent at least below, 3-awned from apical and lateral clefts, the awns mostly 1–3 mm long. *Rachilla* with tufts of hair at the base of the perfect floret and at the base of the awned rudiment. *Second rudiment* (awnless) occasionally produced. *Caryopsis* narrowly obovate, 2.5–3 mm long and ca. 0.5 mm broad.

HABITAT: In extensive pure stands and in mixed prairie associations throughout much of the North American prairie, usually present on rocky, often clayey soils, mainly at elevations from 300–3,000 m.

DISTRIBUTION: Canada (Alberta, Manitoba, Northwest Territories, and Saskatchewan), south through the central and western U.S.A. to Mexico (Aguascalientes, Chihuahua, Coahuila, Distrito Federal, Durango, Guanajuato, Hidalgo, Jalisco, México, Michoacán, Morelos, Nuevo León, Puebla, Querétaro, San Luis Potosí, Sonora, Tamaulipas, Tlaxcala, Veracruz, and Zacatecas). This species also has been reported from scattered localities in the eastern U.S.A. and South America (Argentina) where it probably was introduced.

Bouteloua gracilis (blue grama) and *B. curtipendula* (sideoats grama) are two of the most important range species of the plains regions of North America. Both are widespread throughout the continent and provide a large proportion of the native forage consumed by domesticated animals.

Considerable morphological and cytological variation is exhibited by populations of *B. gracilis* in the western U.S.A. and Mexico. Three levels of ploidy ($2n = 20, 40, 60$) and several aneuploids have been reported.

The collection *Peebles, Harrison & Kearney 6034* (ARIZ, GH) made "near Patagonia Mts." in southern Arizona, 15 September 1929, appears to be of a hybrid plant, possibly a cross betwen *B. gracilis* and *B. hirsuta*. The robust plant has culms to over 1 m tall and thick inflorescence branches 5–7 cm long.

26. **Bouteloua scorpioides** Lag., Gen. & Sp. Nov. 5. 1816. TYPE: Mexico, "Habitat in N. Hisp."—FIG. 29.

Actinochloa scorpioides (Lag.) Roemer & Schultes, Syst. Veg. 2: 420. 1817. *Atheropogon scorpioides* (Lag.) Sprengel, Syst. Veg. 1: 293. 1825. *Chondrosium scorpioides* (Lag.) Kunth, Rév. Gram. 1: 94. 1829.

Tufted *perennial*. *Culms* slender, decumbent-erect or stiffly erect, 20–35 cm tall. *Leaves* mostly basal. Sheaths glabrous. *Ligule* densely short-ciliate. *Blades* narrow, usually involute, 2.5–7(–9) cm long, scaberulous on the adaxial surface. *Inflorescence* with a single unilateral, curved, densely flowered, persistent branch mostly 3.5–5 mm long, this inserted at the culm apex and usually subtended by 2 narrow bracts; branch with 50–90 closely placed and pectinate spikelets. *Spikelets* with a perfect floret below and usually 2 rudimentary florets above, the lower rudiment with a tuft of hair at the base. *Glumes* glabrous, the first ca. 3.3 mm long, the second ca. 5.3 mm long. *Lemma of the perfect floret* 4–5 mm long, bearded at the base and densely pilose on the margins and both sides of the midnerve below the middle, the awns stout, the lateral ones ca. 2 mm long, the central one ca. 1.5 mm long. *Lower rudiment* with awns 4–4.5 mm long. *Caryopsis* obovate, 1.8–2.2 mm long and 0.4–0.5 mm broad.

HABITAT: On rocky slopes and open, grassy plains, mostly at elevations of from 500–3,000 m.

DISTRIBUTION: Central Mexico, reported from Durango, Guanajuato, Hidalgo, Jalisco, México, Nuevo León, Puebla, San Luis Potosí, Tlaxcala, and Zacatecas.

27. **Bouteloua hirsuta** Lag., Varied. Ci. 2(4): 141. 1805.

Short-lived to long-lived, tufted *perennial*, infrequently stoloniferous. *Culms* 15–40(–60) cm tall, moderately branched, with 4–6 elevated nodes. *Leaves* well distributed on the culm. *Sheaths* glabrous or the lowermost somewhat pubescent, pilose at the throat. *Ligule* short, ciliate. *Blades* mostly 1–2 mm broad, flat or subinvolute, sparsely ciliate on the lower margins with papilla-based hairs. *Inflorescence* narrow, with 1–4 short, spreading, densely flowered branches; branches mostly 2.5–4 cm long, with 20–50 sessile, pectinately spreading, subsessile spikelets, the rachis stout, flattened, projecting as a point 5–10 mm beyond the terminal spikelet. *Spikelets* ca. 6 mm long, green to dark purple. *Glumes* slightly unequal, acuminate or tapering to an awn 1–3 mm long, with stiff, papilla-based hairs along either side of the strong midnerve. *Lemma* 3-toothed, more or less puberulent on the back. *Palea* well developed, nearly as long as the lemma. *Rudiments* 2, the lower with 3 hispid awns ca. 4 mm long, the upper a minute scale. *Rachilla* glabrous below the lower rudiment. Anthers yellow or cream-colored, 2–2.5 mm long. *Caryopsis* obovate, 1.5–2 mm long and ca. 0.5 mm broad.

1. Culms glabrous below the nodes ..... 27a. *B. hirsuta* var. *hirsuta*
1′. Culms hispid or papillose-hirsute below the nodes ..... 27b. *B. hirsuta* var. *glandulosa*

27a. **Bouteloua hirsuta** Lag. var. **hirsuta**. TYPE: The type collection of *B. hirsuta* burned with Lagasca's herbarium. A Lagasca specimen in the Madrid Bot. Garden Herbarium (MA) is noted by Griffiths to be representative (see discussion in Griffiths, 1912: 372), and can be considered a lectotype.—FIG. 30.

Actinochloa hirsuta (Lag.) Roemer & Schultes, Syst. Veg. 2: 419. 1817. *Eutriana hirta* Trinius, Gram. Unifl. 240. 1824, based on *Actinochloa hirsuta* Roemer & Schultes.

Bouteloua hirta Lag., Varied. Ci. 2(4): 141. 1805, a garden name mentioned as a synonym of *Bouteloua hirsuta* (fide Griffiths, 1912). *Chondrosium hirtum* (Lag.) H.B.K., Nov. Gen. Sp. Pl. 1: 176, *pl.* 59. 1816, presumably based on *B. hirta* Lag. *Atheropogon hirtus* (Lag.) Sprengel, Syst. Veg. 1: 293. 1825. *Bouteloua hirta* (Lag.) Scribner, Contr. U.S. Natl. Herb. 2: 531. 1894.

Atheropogon papillosus Engelm., Amer. J. Sci. 46: 104. 1843. TYPE: United States, Illinois, Cass Co., *Geyer* in 1842. *Bouteloua papillosa* (Engelm.) Torrey in Marcy, Expl. Red River 300. 1852.

Chondrosium aschenbornianum Nees, Linnaea 19: 692. 1847. TYPE: Mexico, "Aschenb. exs. n. 331." *Bouteloua aschenborniana* (Nees) Griseb. ex Fournier, Mex. Pl. Gram. 2: 137. 1886.

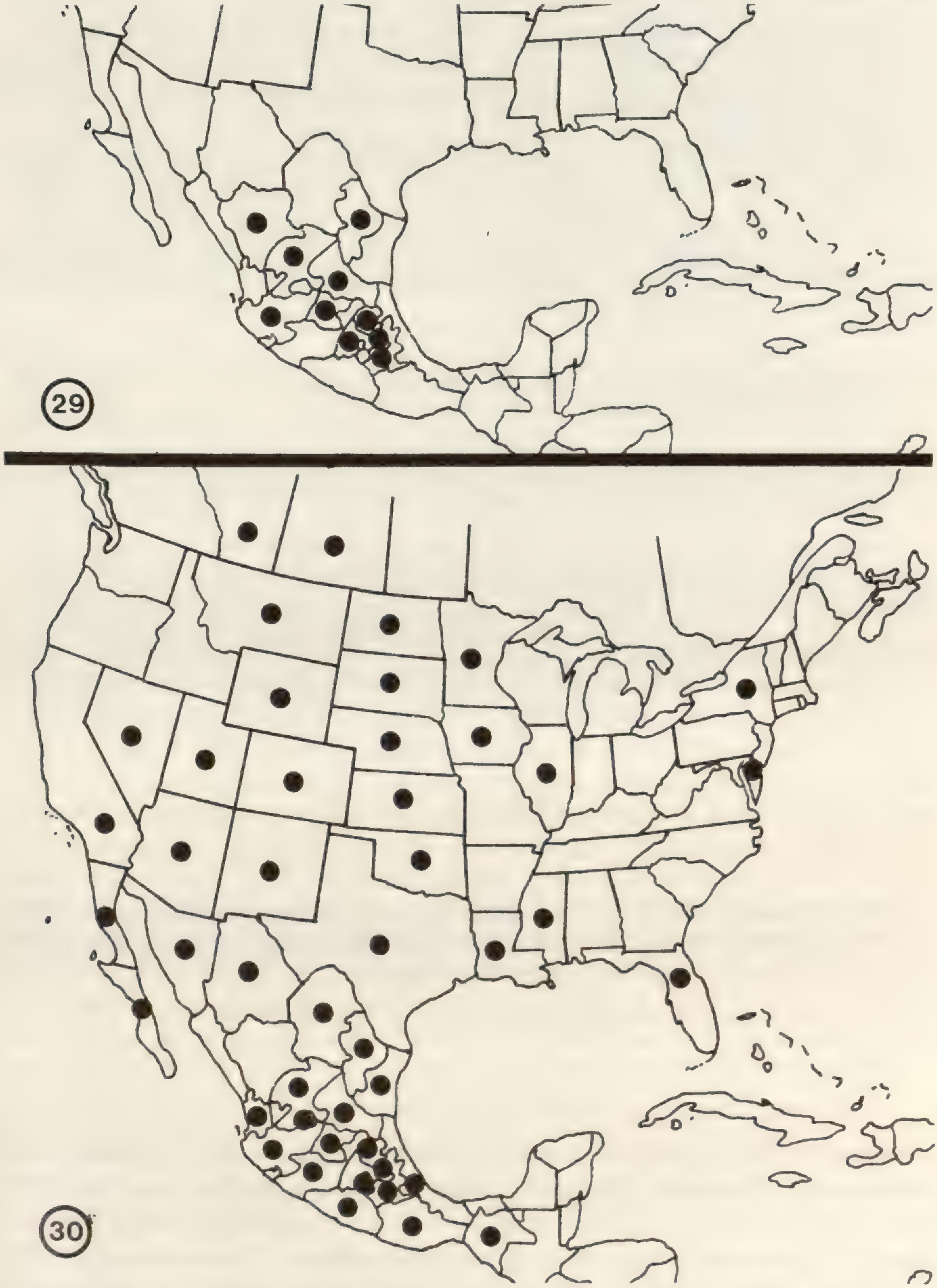
Chondrosium foenum Torrey in Emory, Notes Mil. Reconn. 154, *pl. 12*. 1848. TYPE: United States, ?New Mexico, "Uplands bordering the valley of the Del Norte." *Bouteloua foena* (Torrey) Torrey ex S. Watson & Rothr. in Wheeler, Cat. Pl. Surv. W. 100th Merid. 18. 1874.

Chondrosium drummondii Fournier, Mex. Pl. Gram. 2: 137. 1886. TYPE: United States, Texas, *Drummond 323*.

Bouteloua hirsuta Lag. var. *palmeri* Vasey in Beal, Grasses N. Amer. 2: 417. 1896. TYPE: Mexico, Vasey reports, "Cultivated from seed collected by Palmer in Mexico." 1886."

Bouteloua bolanderi Vasey in Beal, Grasses N. Amer. 2: 417. 1896. TYPE: Mexico, Griffiths (1912) states "It is said to have been cultivated from seed collected by Palmer in Mexico in 1886. I have not been able to find in the National Herbarium any specimen marked as *B. bolanderi*."

Bouteloua hirta Lag. var. *minor* Vasey ex L. H. Dewey, Contr. U.S. Natl. Herb. 2: 531. 1894. TYPE: United States, Texas, "Central Texas."



FIGURES 29–30. Distribution of *Bouteloua* species.—29. *B. scorpioides*.—30. *B. hirsuta* var. *hirsuta*.

HABITAT: Open plains or partially shaded openings in woods and brush, on well-drained, usually rocky soils at from 50 m or less to 300 m.

DISTRIBUTION: Saskatchewan and Alberta, south throughout almost all of the U.S.A. east of the Rocky Mountains, to Florida, Louisiana, Texas, New Mexico, Arizona and southern California, and through most of Mexico (22 states and south to southern Chiapas).

In the northern portion of its range, *B. hirsuta* tends to be slender, short in stature, and with 1 or 2 inflorescence branches, whereas in the south the plants tend to be tall and stout, and often have 3–4 inflorescence branches. For the most part, the plants of central and southern Mexico are tall, coarse, and long-lived. Here both *B. hirsuta* and *B. gracilis* are mostly large, bunch-type plants, similar to each other in general appearance.

27b. **Bouteloua hirsuta** Lag. var. **glandulosa** (Cerv.) Gould, J. Arnold Arb. 60: 320. 1979.—FIG. 31.

Erucaria glandulosa Cerv., Naturaliza 1: 347. 1870. TYPE: Mexico, "Guadelupe et Moctezuma."
Bouteloua hirticulmis Scribner, U.S.D.A. Div. Agrostol. Circ. 30: 4. 1901. TYPE: Mexico, Baja California Sur, Sierra de San Francisquito, *Brandegee 11*.

Plants generally similar to *B. hirsuta* var. *hirsuta* but the lower internodes densely hispid with long hairs, these often papilla-based, the lower nodes minutely puberulent.

HABITAT: Dry rocky slopes.

DISTRIBUTION: United States: Arizona: Puna Co., Lochiel, *Goodding A9837* (US). Santa Cruz Co., Pera Blanca, *Goodding, Hardies & Crafts 3582* (US). Mexico: Several locations in the states of Aguascalientes, Baja California Sur, Chiapas, Chihuahua, Guerrero, Hidalgo, Jalisco, México, Morelia, Nayarit, Oaxaca, Veracruz, and Zacatecas. Guatemala: Dept. Huehuetenango, *Steyermark 51472* (US).

28. **Bouteloua pectinata** Featherly, Bot. Gaz. (Crawfordsville) 91: 103. 1931. TYPE: United States, Oklahoma, Comanche County, near Fort Sill, 17 Aug. 1929, *B. English 71* (US, holotype).—FIG. 32.

Bouteloua hirsuta Lag. var. *pectinata* (Featherly) Cory, Rhodora 38: 405. 1936.
Bouteloua hirsuta Lag. var. *major* Vasey, U.S.D.A. Div. Bot. Bull. 12: *pl. 39, fig. 3*. 1890, without description. TYPE: United States, Texas, Travis County, Austin, *E. P. Stiles* in 1884 (US, holotype). *Bouteloua hirta* (H.B.K.) Scribner var. *major* (Vasey) Vasey ex L. H. Dewey, Contr. U.S. Natl. Herb. 2: 531. 1894.

Strong *perennial* with stiffly erect culms from a firm base. *Rhizomes* and *stolons* absent. *Culms* 35–75 cm tall, unbranched above the base, usually with 3 nodes. *Leaves* mostly in a basal clump, those of the upper culm nodes greatly reduced. *Lower sheaths* pubescent, pilose at the throat. *Ligule* a short, ciliate membrane. *Blades* firm, curved, involute, 15–30 cm long and ca. 2 mm wide, ciliate with papilla-based hairs on the lower margins, attenuate at the tip. *Inflorescence* 25–45 cm long, usually with 3–5 branches; branches mostly 3–4 cm long, with 40–50 spikelets, the *rachis* projecting as a point beyond the terminal

spikelet. *Spikelets* as in *B. hirsuta* but the anthers ca. 3 mm long. *Caryopsis* 1.5–2 mm long.

HABITAT: On rocky, usually limey, slopes and outcrops, at elevations of 60–500 m.

DISTRIBUTION: From Pontotoc and Comanche counties, Oklahoma, south to Uvalde County, Texas. *Bouteloua pectinata* has been reported from 27 Texas counties, with the eastern limit being in Medina and Milam counties and the western limit in Wilbarger County and the western portion of Edwards County.

Relationships of *B. pectinata* and *B. hirsuta* have been discussed by Roy & Gould (1971). *Bouteloua pectinata* is a diploid ($2n = 20$) that grows only on well-drained, relatively undisturbed limey soils, most frequently on thin-soiled limestone outcrops. Flowering mainly in July and August, *B. pectinata* has a much shorter period of anthesis than *B. hirsuta*. The morphological uniformity of this species contrasts strikingly with the variability observed in populations of plants of *B. hirsuta*.

29. **Bouteloua eriopoda** (Torrey) Torrey, U.S. Expl. Miss. Pacif. Rep. 4: 155. 1856.—FIG. 33.

Chondrosium eriopodum Torrey in Emory, Notes Mil. Reconn. 154. 1848. TYPE: United States, New Mexico: "abundant along the Del Norte [Rio Grande] and in the region between that river and the waters of the Gila," no collection cited; selected as a neotype is *Wooton 458* (US) which Griffiths (1912) stated to be typical.

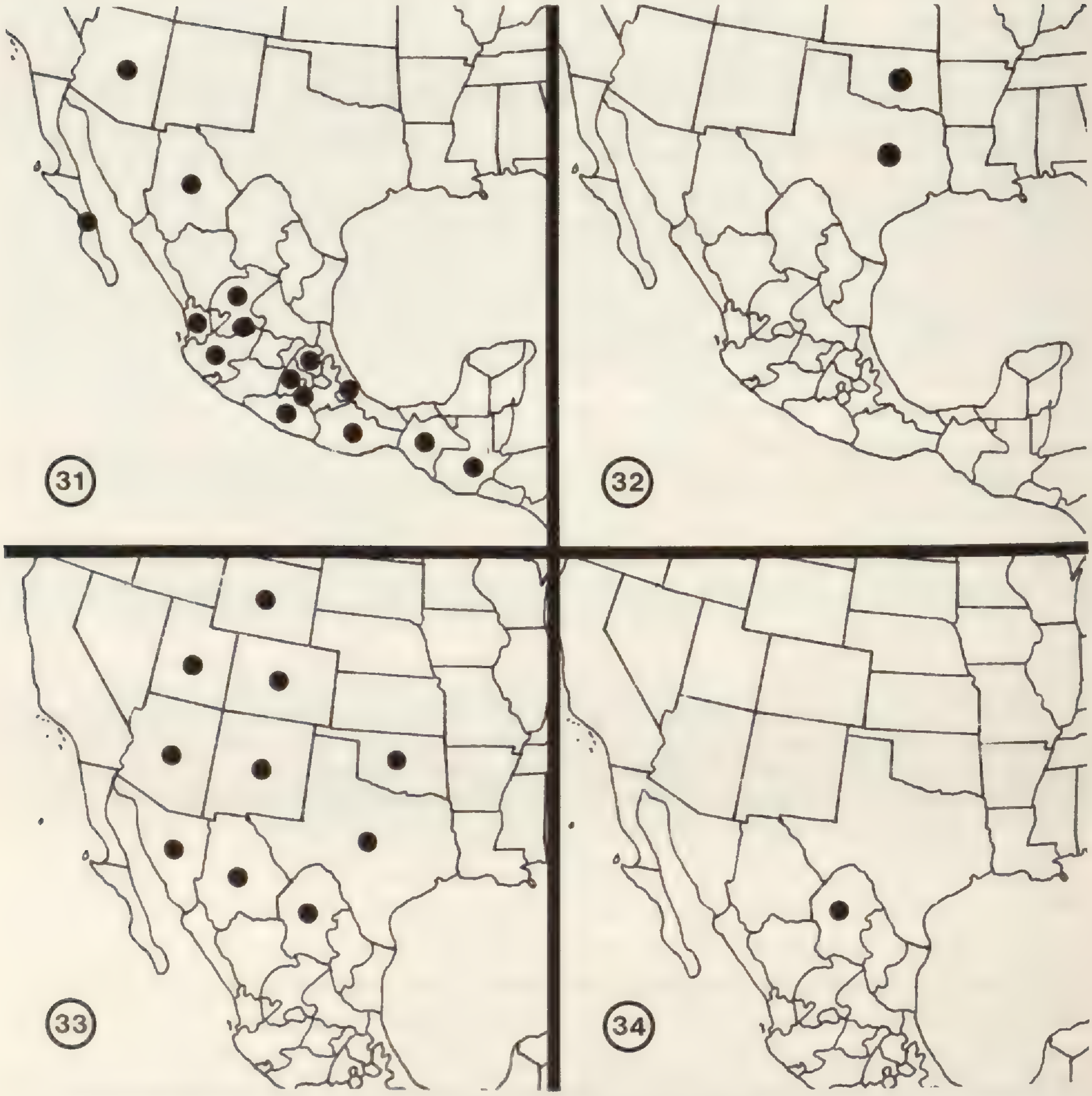
Bouteloua brevifolia Buckley, Proc. Acad. Nat. Sci. Philadelphia 1862: 93. 1862. TYPE: United States, Texas, "Northwestern Texas," *Wright 748* (US, isotype).

Perennial. Culms wiry, mostly 20–60 cm tall, from a knotty base, typically decumbent and stoloniferous below, wooly-pubescent on the lower internodes and stolons. *Leaves* inconspicuous, with short blades and sheaths much shorter than the internodes. *Ligule* a minute fringed membrane. *Blades* thin, flat or folded, 0.5–2 mm broad. *Inflorescence* branches 3–8, slender, persistent, widely spaced, mostly 2–5 cm long, with 8–18 nonpectinate spikelets, the branch rachis densely white-wooly at the base. *Spikelets* with 1 perfect floret and 1 awned rudiment on a long stipe. *Glumes* unequal, glabrous or scabrous, acute or acuminate, the second mostly 6–9 mm long. Lemma bearded at the base, glabrous or sparsely puberulent above, tapering above to a stout terminal awn mostly 1.5–3 mm long and much-reduced lateral awns. *Rudiment* with 3 awns 4–8 mm long, usually bearded at the firm, nonmembranous base. *Caryopsis* narrowly elliptic-obovate, 2.5–3 mm long.

HABITAT: On dry plains, foothills, and open forested slopes often associated with shrubs and subshrubs. Growing mostly at 1,000–1,800 m elevation but occasionally present to 2,500 m.

DISTRIBUTION: Wyoming, Colorado, and Utah, south to Oklahoma, Texas, New Mexico, Arizona, and northern Mexico.

Bouteloua eriopoda (black grama) is a highly palatable forage grass, stated by the *Range Plant Handbook* (U.S. Forest Service, 1937) to be the original mainstay of the range on numerous areas of the Southwest. Under heavy grazing



FIGURES 31–34. Distribution of *Bouteloua* species.—31. *B. hirsuta* var. *glandulosa*.—32. *B. pectinata*.—33. *B. eriopoda*.—34. *B. eriostachya*.

pressure this grass is drastically reduced in stand and persists only in the protection of shrubby plants and cacti.

30. **Bouteloua eriostachya** (Swallen) J. R. Reeder, Bull. Torrey Bot. Club 94: 7. 1967.—FIG. 34.

Bouteloua eriopoda (Torrey) Torrey var. *eriostachya* Swallen, Proc. Biol. Soc. Wash. 56: 81. 1943. TYPE: Mexico, Coahuila, vicinity of Aguaje de Pajarito, canyon at west end of Sierra de la Fragua, *I. M. Johnston 8718* (GH, US, isotypes).

Strong *perennial*. *Culms* erect, 40–60 cm tall from a knotty base. *Stolons* apparently not developed. *Lower culm internodes* conspicuously lanate. *Ligule* a minute, fringed membrane. *Blades* thin and narrow, mostly 0.5–2 mm broad. *Inflorescence* branches 3–8, widely spaced, persistent, mostly 2–5 cm long, with

8–12 nonpectinate spikelets, the branch rachis densely white-wooly at the base. *Spikelets* with 1 perfect floret and 1 awned rudiment on a long stipe. *Glumes* glabrous or scabrous, acute or acuminate, the second 6–9 mm long, the first shorter. *Lemma* bearded at the base, glabrous or sparsely puberulent above, tapering above to a stout terminal awn mostly 1.5–3 mm long and much-reduced lateral awns. Rudiment with 3 awns 4–8 mm long, usually bearded at the firm, nonmembranous base. *Caryopsis* narrowly elliptic-obovate, 2.5–3 mm long.

HABTAT: Locally frequent on dry, rocky flats.

DISTRIBUTION: Endemic to western Coahuila, Mexico. Known to me only from the type collection and the following five records: Vicinity of Santa Elana mines, Sierra de las Cruces, *Johnston* & *Muller 245, 806, 1021* (all US). San Antonio de los Alamos, E base of the Sierra de San Antonio, *Johnston* 8257 (US). 19 mi S of Cuatro Cienegas, *Reeder* & *Reeder 4522* (US).

In describing this taxon as a variety of *B. eriopoda*, Swallen (1943) noted, "*Bouteloua eriopoda* (Torrey) Torrey *gluma secunda villosa differt*. This variety closely resembles the species, differing primarily in having the second glumes rather densely villous. The structure of the spikelets is identical. The specimens at hand do not show any indication that the plants are stoloniferous, but this character is not always evident in the specimens. The culms are a little more conspicuously lanate than in the species."

In elevating the *eriostachya* taxon to specific rank, Reeder (1967) noted that it is hexaploid ($2n = 60$) rather than diploid as in *B. eriopoda*, that it seems to be strictly caespitose rather than stoloniferous, that the culms are more conspicuously lanate than in *B. eriopoda*, and that the branch rachis and second glumes are villous to lanate rather than glabrous.

31. **Bouteloua trifida** Thurb. in S. Watson, Proc. Amer. Acad. Arts 18: 177. 1883. TYPE: Mexico, Coahuila, Monclova, 1880, *Palmer 1355* (GH, holotype; NY, fragment US, isotypes).—FIG. 35.

Bouteloua burkii Scribner in S. Watson, Proc. Amer. Acad. Arts 18: 179. 1883. TYPE: United States, western Texas and New Mexico, *Berlandier 167* (GH, K, syntypes) and *1427* (GH, syntype). *Bouteloua trifida* var. *burkii* Vasey ex L. H. Dewey, Contr. U.S. Natl. Herb. 14: 387. 1912.

Chondrosium trinii Fournier, Mex. Pl. Gram. 2: 136. 1886. TYPE: United States, Texas, Webb Co., Laredo, *Berlandier 1427* (K, isotype). *Chondrosium polystachyum* Trinius ex Fournier, Mex. Pl. Gram. 2: 136. 1886, as a synonym of *Chondrosium trinii* Fournier. *Bouteloua trinii* (Fournier) Griffiths, Contr. U.S. Natl. Herb. 14: 387. 1912.

Chondrosium virletii Fournier, Mex. Pl. Gram. 2: 136. 1886. TYPE: Mexico, San Luis Potosí, *Virlet 1373*.

Tufted *perennial*. *Culms* slender, wiry, (8–)10–30(–40) cm long from a firm, often somewhat rhizomatous base. *Leaves* mostly in a basal clump, glabrous, scabrous, or puberulent. *Ligule* a minute fringed membrane. *Blades* flat or loosely infolded, mostly 4–8 cm long and 1.5 mm or less broad. *Inflorescence* 3–9 cm long, with 2–7 slender, persistent branches; branches 12–25 mm long including the awns, with 8–24(–32) spikelets. *Spikelets* with 1 rudimentary floret above the perfect one. *Glumes* slightly unequal, glabrous, acute, acuminate, or mucronate from a slightly bifid apex. *Lemma* 2 mm long, glabrous or with hairs not

over 0.5 mm long at the base, the awn about twice as long as body. *Rudimentary floret* with a short awn column and awns 3.5–6 mm long. *Caryopsis* narrowly elliptic, ca. 1 mm long and 0.4 mm broad.

HABITAT: Dry plains and rocky slopes, mostly at elevations of 300–1,500 m.

DISTRIBUTION: Southern Utah, central and western Texas (reported from 47 counties), New Mexico, Arizona, Nevada (Clark Co.), southern California (Inyo Co.), and central Mexico. Reported from the following states of Mexico: Chihuahua, Coahuila, Guanajuato, Nuevo León, San Luis Potosí, and Tamaulipas.

Bouteloua trifida (red grama) is a low, tough, drought-resistant species that provides a limited amount of forage during the early part of the growing season.

32. **Bouteloua kayi** Warnock, Field & Lab. 23: 15. 1955. TYPE: United States, Texas, Brewster Co., near Rio Grande River, "in limestone crevices on lower portion of Maravillas Creek," 4 Aug. 1954, *Lamar Kay K-1* (SMU, isotype). —FIG. 36.

Tufted *perennial.* Culms stiffly erect, mostly 20–40(–50) cm tall. *Leaves* glaucous, mostly basal, scabrellous to glabrous. *Ligule* a minute fringed membrane. *Blades* involute, scabrellous on the adaxial surface, 1–1.5 mm broad. *Inflorescence* with 7–15(–20) slender, erect branches mostly 1.5–3 cm long; branches with 7–14(6–20) widely spaced spikelets on pedicels mostly 0.6–0.8 mm long. *Spikelets* 6–8 mm long including the awns, with a single reduced floret above the perfect one. *Disarticulation* above glumes. *Glumes* nearly equal, glabrous, 2.5–4 mm long, acute or bidentate at the apex, awnless or the stout midnerve extending as a short awn. *Lemma* with 3 stout, nearly equal awns, these mostly 3–4 mm long and ⅓–¼ longer than the glabrous or sparsely strigose body, the central awn from between 2 teeth 0.4–0.6 mm long. *Rudiment* a reduced lemma with stout awns similar in size to those of the lower floret on a minutely lobed, much-reduced membranous base, the rudiment and rachilla both glabrous.

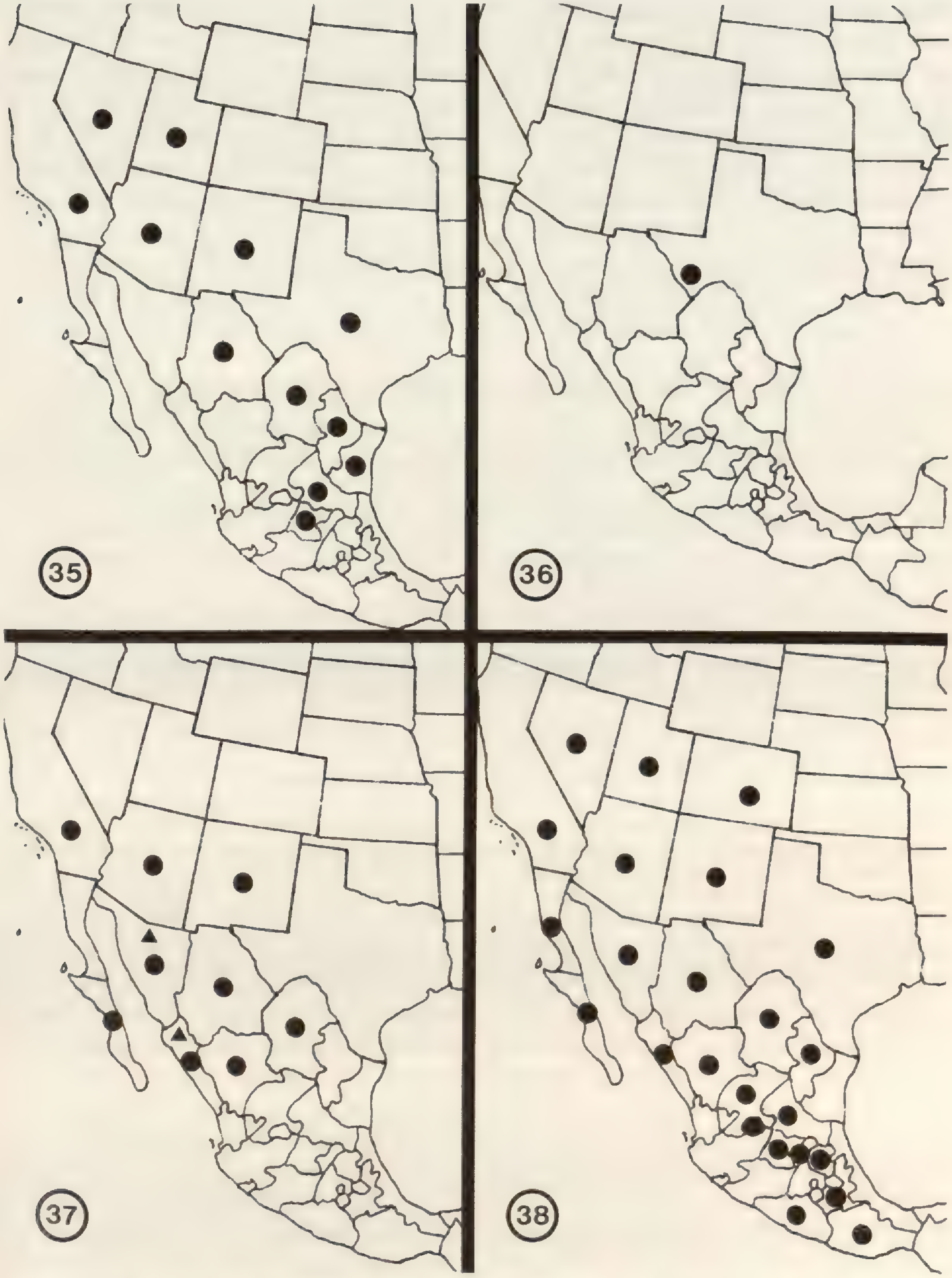
HABITAT. Rocky, exposed slopes, at elevations of 2,200–2,500 m.

DISTRIBUTION: Known only from Boquillas Canyon of the Big Bend National Park in southern Brewster County, Texas. Recorded collections other than the type: Brewster Co.: Overton Ranch, *Kay & Burleson*, 2 Feb. 1954 (US). Black Gap, W slope of Maravillas Creek, *Warnock 12342* (TAES).

A species close to *B. trifida* but differing in several characters. *Bouteloua kayi* has stouter, strictly erect culm bases and fewer expanded culm internodes and elevated nodes. The inflorescence branches are more numerous and longer, on the average. The lemma awns are generally shorter than in *B. trifida* and the lemma body is longer.

33. **Bouteloua barbata** Lag., Varied. Ci. 2(4): 141. 1805.

Tufted *annual* or *perennial.* *Culms* erect or decumbent-spreading. *Leaves* short, mostly basal. *Sheaths* with tufts of long hairs on either side of the collar. *Ligule* a short, fringed membrane. *Blades* 1.5–7 mm long, 1–3(–4) mm broad, often scabrous and sparsely strigose on the adaxial surface and with a few long



FIGURES 35–38. Distribution of *Bouteloua* species.—35. *B. trifida*.—36. *B. kayii*.—37. *B. barbata* var. *rothrockii* (solid circles) and *B. barbata* var. *sonorae* (solid triangles).—38. *B. barbata* var. *barbata*.

hairs above the ligule. *Inflorescence* with (2–)4–8(–9) persistent branches; branches usually 1–3 cm long, with 25–40 closely placed and pectinately spreading spikelets, the rachis glabrous or minutely scabrous. *Spikelets* 2.5–4 mm long including the short awns, usually with 2 rudiments above the perfect floret. *Glumes* glabrous, acute, acuminate or slightly notched and mucronate at the apex. *Rachilla* with a tuft of hairs below the awned rudiment. *Lemma* of the perfect floret densely pubescent at least on the margins, 3-lobed and 3-awned, the awns 0.5–3 mm long. *Lower rudiment* with rounded lobes and 3 awns about as long as those of lemma. *Upper rudiment* minute, awnless, fan shaped. *Caryopsis* obovate, pointed at the base, variable in size but usually ca. 1 mm long.

1. Plants annual, the culms usually geniculate-spreading at the base, occasionally rooting at the lower nodes ..... 33a. *B. barbata* var. *barbata*
1′. Plants perennial.
   2. Base of plant hard and "knotty"; culms spreading at the base and often developing long stolons ..... 33b. *B. barbata* var. *sonorae*
   2′. Base of plant not hard and "knotty," weakly perennial in appearance; culms erect from the base, not stoloniferous ..... 33c. *B. barbata* var. *rothrockii*

33a. **Bouteloua barbata** Lag. var. **barbata**. TYPE: Mexico.—FIG. 38.

Actinochloa barbata (Lag.) Roemer & Schultes, Syst. Veg. 2: 420. 1817. *Eutriana barbata* (Lag.) Kunth, Rév. Gram. 1: 96. 1829.

Chondrosium polystachyum Bentham, Bot. Voy. Sulph. 56. 1844. TYPE: Mexico, Baja California Sur, Magdalena Bay, *Barclay* (US, holotype fragment; BM, isotype). *Bouteloua polystachya* (Bentham) Torrey, U.S. Expl. Miss. Pacif. Rep. 5(2): 366, *pl. 10*. 1857.

Chondrosium subscorpioides C. Mueller, Bot. Zeitung (Berlin) 14: 347. 1856. TYPE: Mexico, Baja California, *Barclay*.

Bouteloua pumila Buckley, Proc. Acad. Nat. Sci. Philadelphia 1862: 93. 1862. TYPE: United States, Texas, *Wright 754* (GH, US, isotypes).

Erucaria tetrastachya Cerv., Naturaliza 1: 349. 1870. TYPE: Mexico.

Chondrosium exile Fournier, Mex. Pl. Gram. 2: 137. 1886. TYPE: Mexico, *Berlandier 842*.

Chondrosium microstachyum Fournier, Mex. Pl. Gram. 2: 138. 1886. TYPE: Mexico, Guadeloupe, *Bourgeau 667* (US, isotype). *Bouteloua microstachya* (Fournier) L. H. Dewey, Contr. U.S. Natl. Herb. 2: 531. 1894.

Bouteloua arenosa Vasey, U.S.D.A. Div. Bot. Bull. 12(1): *pl. 34*. 1890. TYPE: Mexico, Guaymas, 1887, *Palmer 189* (US, isotype).

Bouteloua micrantha Scribner & Merrill, U.S.D.A. Div. Agrostol. Circ. 32: 8. 1901. TYPE: United States, Arizona, Pima Co., Fort Lowell, *Griffiths 1556* (US, holotype).

Short-lived *annual* of exceedingly variable size and general aspect. *Culms* typically spreading but erect in dense vegetation, commonly 6–30 cm long, never developing extensive stolons. *Leaf blades* mostly 1–1.5 mm broad.

HABITAT: Usually on loose sands of valley flats, rocky slopes and washes, often on disturbed soils, mostly at 2,000 m or lower.

DISTRIBUTION: Southern Colorado, Utah, Nevada, and California, south through Mexico to Guerrero. Reported from 32 counties of central and western Texas, 13 counties of New Mexico, and in all counties of Arizona except Apache. In Mexico *B. barbata* has been collected in the states of Aguascalientes, Baja California Norte, Baja California Sur, Chihuahua, Coahuila, Durango, Guanajuato, Guerrero, Hidalgo, Nuevo León, Oaxaca, Puebla, Querétaro, San Luis Potosí, Sinaloa, Sonora, and Zacatecas.

Plants of the common and widespread *Bouteloua barbata* var. *barbata* fre-

quently are confused with seedlings of *B. trifida* when the perennial habit of the latter is not evident. The following is a comparison of differences between the two:

B. barbata var. *barbata*	*B. trifida*
1. Glumes short-awned from a conspicuously notched apex.	1. Glumes acuminate or mucronate from a slightly notched apex.
2. Awn of lemma about as long as the body.	2. Awn of lemma about twice as long as the body.
3. Lemma conspicuously hairy, the hairs to 1 mm long.	3. Lemma inconspicuously hairy, the hairs to 0.5 mm long.
4. Inflorescence branches often 2–2.5 mm long.	4. Inflorescence branches usually less than 2 cm long.
5. Culms usually decumbent and widely spreading at the base.	5. Culms erect or slightly curving-erect at the base.
6. Plants usually without a dense tuft of basal leaves.	6. Culms with a dense tuft of basal leaves.
7. Annual.	7. Perennial (but seedlings flowering in the first year).

33b. **Bouteloua barbata** Lag. var. **sonorae** (Griffiths) Gould, comb. nov.

Bouteloua sonorae Griffiths, Contr. U.S. Natl. Herb. 14: 389. 1912. TYPE: Mexico, Sonora, Yaqui River, *Palmer* in 1869 (US, holotype).

Perennial. Culms erect or geniculate-spreading from a hard "knotty" base, slender, often wiry, frequently developing stolons to 50 cm long, the erect culms 10–25(–60) cm tall.

HABITAT: In sandy soil, on open coastal flats or on dry, open or brushy slopes at low elevations.

DISTRIBUTION: Known only from Sonora and Sinaloa, Mexico. I have seen the following collections: Sonora: 10 mi S of Nogales, *Beetle et al. M-1909* (TAES). San Bernardo, *Gentry, Barclay & Arguelles 19253* (US). Mazatlán Hwy. N of Río Piaxtla, *Gould 12116* (TAES). Guaymas, *Hitchcock 3552* (US); *A. Chase 5509* (US). Alamos, *Palmer 751* in 1890 (US). Sinaloa: Mazatlán River, *W. G. Wright 1322* (US). Ymala, *Palmer 1761* (US). Culiacán, *Rose, Standley & Russell 14872* (US). Río Humayo at Culiacancito, *Gentry, Barclay & Arguellas 19452* (US).

Bouteloua sonorae Griffiths was maintained as a separate species by Hitchcock (1919), Hitchcock et al. (1939), and Swallen (1964). In the original description, Griffiths (1912) stated that, "this species to be looked upon as a perennial *B. barbata*, a native of the west coast of northern Mexico." Neither Hitchcock nor Swallen attempted a further comparison with *B. barbata* var. *barbata*.

33c. **Bouteloua barbata** Lag. var. **rothrockii** (Vasey) Gould, comb. nov.—FIG. 37.

Bouteloua rothrockii Vasey, Contr. U.S. Natl. Herb. 1: 268. 1893. TYPE: United States, Arizona, Yavapai Co., Cottonwood, *Rothrock 347* (US, holotype; GH, isotype).

Bouteloua polystachya (Bentham) Torrey var. *major* Vasey in Wheeler, Rep. U.S. Surv. 100th Merid. 6: 287. 1878. TYPE: United States, Arizona, Santa Cruz Co., Sonoita Valley, *Rothrock 691* (US, holotype; GH, isotype).

Short-lived *perennial*. *Culms* usually 25–60(–75) cm tall, usually in small tufts or clumps, stiffly erect or slightly geniculate-spreading below. *Blades* glabrous or sparsely hirsute with papilla-based hairs, 1–3(–4) mm broad, often loosely involute. *Inflorescence* branches (3–)4–8, per culm, mostly 1.5–3 cm long and ca. 3 mm broad excluding awns. *Spikelets* usually 35–50 per branch, ca. 5 mm long.

HABITAT: On dry slopes and sandy flats, mostly at 750–1,700 m elevation.

DISTRIBUTION: New Mexico (Hidalgo and Luna counties), Arizona (Cochise, Coconino, Gila, Graham, Pima, Pinal, Santa Cruz, Yavapai, and Yuma counties), California (*Coulter 792* [GH] without locality), and Mexico (states of Baja California Sur, Chihuahua, Coahuila, Durango, Sinaloa, and Sonora).

In southern New Mexico and southern Arizona, *B. barbata* var. *barbata* and *B. barbata* var. *rothrockii* frequently grow together and, in the field, often are readily distinguishable on the basis of growth habit. On open ground, the culms of *B. barbata* var. *barbata* are conspicuously decumbent-spreading at the base and the erect portion of the culm is relatively short. In the same habitat, *B. barbata* var. *rothrockii* has a stiffly erect habit and usually taller culms. In Mexico the habit differences become less evident and, especially in the southern portion of the range, there is no consistent difference between the two, especially on the basis of herbarium specimens.

34. **Bouteloua simplex** Lag., Varied. Ci. 4: 141. 1805. TYPE: Peru.—FIG. 39.

Actinochloa simplex (Lag.) Roemer & Schultes, Syst. Veg. 2: 418. 1817. *Chondrosium simplex* (Lag.) Kunth, Rév. Gram. 94. 1829.

Chloris procumbens Durand, Chlor. Sp. 16. 1808. TYPE: Grown at Madrid from seed collected by Née. The seed is said to have come from the Philippine Islands (where the species does not occur) but must have come from South America or Mexico, which Née visited. *Chondrosium procumbens* (Durand) Desvaux ex Beauvois, Ess. Agrost. 41: 158. 1812. *Atheropogon procumbens* (Durand) Jacq. f., Ecol. Gram. 16. 1813. *Actinochloa procumbens* (Durand) Roemer & Schultes, Syst. Veg. 2: 417. 1817. *Cynodon procumbens* (Durand) Rasp., Ann. Sci. Nat. (Paris) 5: 303. 1825. *Bouteloua procumbens* (Durand) Griffiths, Contr. U.S. Natl. Herb. 14: 364. 1912.

Chloris filiformis Poir. in Lam., Encycl. Suppl. 2: 237. 1811, not *Chloris filiformis* (Vahl) Poir. TYPE: Based on plant grown at Paris. *Chloris tenuis* Poir. in Lam., Encycl. Suppl. 5: 614. 1817, as synonym of *C. filiformis*.

Bouteloua prostrata Lag., Gen. & Sp. Nov. 5. 1816. TYPE: Mexico. *Actinochloa prostrata* (Lag.) Roemer & Schultes, Syst. Veg. 2: 419. 1817. *Chondrosium prostratum* (Lag.) Sweet, Hort. Brit. 1: 175, *pl.* 56. 1816.

Chondrosium humile H.B.K., Nov. Gen. Sp. Pl. 1: 175, *pl.* 56. 1816. TYPE: Ecuador, "Crescit in frigidus exsiccatis, argillosis propter Llactacunga Quitensium et in monte Guadelupensi . . . ," *Humboldt & Bonpland*. *Actinochloa humilis* (Beauvois) Willd., Roemer & Schultes, Syst. Veg. 2: 417. 1817. *Eutriana humilis* (Beauvois) Trinius, Gram. Unifl. 239. 1824. *Atheropogon humilis* (Beauvois) Sprengel, Syst. Veg. 1: 293. 1825. *Bouteloua humilis* (Beauvois) Hieron., Bol. Acad. Nat. Ci. 4: 495. 1882.

Chondrosium tenue Beauvois ex H.B.K., Nov. Gen. Sp. Pl. 1: 176, *pl.* 57. 1816. TYPE: Mexico, *Humboldt & Bonpland*. *Actinochloa tenuis* (Beauvois ex H.B.K.) Willd. ex Roemer & Schultes, Syst. Veg. 2: 418. 1817. *Eutriana tenuis* (Beauvois ex H.B.K.) Trinius, Gram. Unifl. 240. 1824. *Bouteloua tenuis* (Beauvois ex H.B.K.) Grisebach, Abh. Königl. Ges. Wiss. Göttingen 19: 259. 1874.

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FIGURE 39. Distribution of *Bouteloua simplex*.

Erucaria lutescens Cerv., Naturaliza 1: 349. 1870. TYPE: Mexico.
Bouteloua pusilla Vasey, Bull. Torrey Bot. Club 11: 6. 1884. TYPE: United States, New Mexico, Kingman, *Vasey* in June 1881 (US, isotype).
Bouteloua brachianthera Philippi, Anales Mus. Nac. Chile Bot. 8: 85. 1891. TYPE: Chile, Prov. Tarapaca.

Bouteloua rahmeri Philippi, Anales Mus. Nac. Chile Bot. 8: 85. 1891. TYPE: Chile, Prov. Tarapaca (photo in US). *Bouteloua simplex* Lag. var. *rahmeri* (Philippi) Henr., Meded. Rijks-Herb. 40: 66. 1921.

Tufted *annual*. *Culms* decumbent-spreading or less frequently erect, 3–20 (–35) cm long. *Sheaths* glabrous. *Ligule* a minute, fringed membrane. *Blades* mostly 2–8 cm long and 0.5–1.5 mm broad, flat or involute, often pilose on the adaxial surface and ciliate on the margins above the ligule. *Inflorescence* a unilateral spike (actually a single terminal branch), mostly 1–2.5 cm long, with 30–80 closely placed, pectinate spikelets. *Spikelets* with 2, occasionally only 1, rudimentary florets. *Rachilla* with tufts of hair below the perfect floret and below the first rudiment. *Disarticulation* at a rounded, knoblike callus at the base of the perfect floret. *Glumes* glabrous or scabrous near the tip, acute or acuminate, the first about half as long as the second, the second 3.5–5 mm long. *Lemma* silky pubescent on the nerves, the body 2.5–3.5 mm long, the nerves extending as short, stout, flattened awns, the terminal one projecting between 2 membranous lobes ca. 1 mm long. *Lower rudiment* with 3 stout awns 1–2 mm long and a stout awn column, the membranous body vestigial or lacking. *Upper rudiment*, when present, a minute fan-shaped scale. *Caryopsis* obovate, 1.8–2 mm long.

HABITAT: Dry plains, washes and rocky slopes, mostly at elevations of 1,200–2,500 m.

DISTRIBUTION: In North America, southern Colorado and Utah, western Texas, New Mexico, Arizona, and south through Central America; in South America, at medium altitudes from Colombia, Ecuador and Peru through Bolivia to Chile and Argentina.

The long list of synonyms for *B. simplex* attests to the wide distribution and variability of this economically unimportant annual. In North America it is recorded from Colorado (Archuleta, El Paso, La Plata, and Las Animas counties), Utah (Garfield Co.), Texas (Jeff Davis Co.), New Mexico (Colfax, Grant, Lincoln, Rio Arriba, San Juan, San Miguel, Santa Fe, Sierra, and Socorro counties), Arizona (Apache, Coconino, Gila, and Yavapai counties) and Mexico (states of Baja California Sur, Chihuahua, Coahuila, Distrito Federal, Durango, Guanajuato, Hidalgo, Jalisco, San Luis Potosí, Sonora, and Zacatecas).

Bouteloua simplex is especially well represented in all of the countries on the western side of South America from Colombia to Argentina.

35. **Bouteloua elata** Reeder & Reeder, Brittonia 15: 215. 1963. TYPE: Mexico, Colima, ca. 13 mi SW of Ciudad Colima, *Reeder & Reeder 2356* (RM, holotype; GH, US, isotypes).—FIG. 40.

Perennial. *Culms* stiffly erect from a hard, woody base, glabrous, unbranched above the base, 70–120(–140) cm tall. *Sheath* glabrous or with a few hairs on the margins at the apex. *Ligule* reduced to a fringe of hair ca. 0.5 mm long. *Blades* narrow, flat, folded or loosely involute, tapering to a fine point, the lower ones 20–50 cm long and 3–4 mm broad, usually with a tuft of long hairs just above the ligule. *Inflorescence* to 40 cm long, usually with 9–30 widely spaced branches; branches 2–8 cm long, with 40–100 or more closely placed, pectinate spikelets, the

rachis ciliate on the margins with silvery, papilla-based hairs 2–3 mm long. *Spikelets*, including awns, 4.5–5 mm long, with a perfect, bisexual lower floret, and a 3-awned rudiment above. *Spikelets* occasionally with a vestigial scalelike third floret above the awned rudiment. *Glumes* slightly unequal, the first shorter, both glumes short awned from a notched bifid apex, the second glume with a few silvery, papilla-based, hairs on the nerve. *Lemma of the lower floret* with a deeply lobed body 2–2.5 mm long and 3 awns 2–4 mm long, the body appressed-pubescent below. *Palea* of the lower floret well developed, with the 2 nerves extending as short awns. Caryopsis obovate, ca. 1 mm long and 0.4 mm thick.

HABITAT: On rocky slopes and outcrops, often in partial shade, at elevations of 400–800 m.

DISTRIBUTION: Endemic to southern Mexico, known from several collections in the vicinity of Colima, and from several collections in central Chiapas.

An attractive low perennial bunchgrass with conspicuous bright orange anthers.

36. **Bouteloua parryi** (Fournier) Griffiths, Contr. U.S. Natl. Herb. 14: 381. 1912.

Tufted *annual* or stoloniferous, short-lived *perennial* with mostly basal leaves. *Ligule* a short, fringed membrane. *Leaves* more or less papillose-hispid or hirsute. *Blades* short, 1–2(–3) mm long. *Inflorescence* branches mostly 3–6 but occasionally only 1–2 on short, late-formed or depauperate culms; branch rachis mostly with 25–60 closely placed, pectinate spikelets, with a spikelet at or very near the tip. *Disarticulation* above glumes, the inflorescence branch rachis persistent; margins of the branch rachis and midnerve of the second glume ciliate with silvery, mostly papilla-based hairs. *Spikelet* with 1 perfect lower floret and 2 neuter, rudimentary florets, the uppermost reduced to a scale. *Caryopsis* obovate, pointed at both ends, 1.1–1.5 mm long and 0.4–0.5 mm thick.

1. Plants annual, not stoloniferous; culms slender but not wiry; blades frequently 2 mm broad; inflorescence branches, at least some, 2 cm or more long ..... 36a. *B. parryi* var. *parryi*
1′. Plants perennial (or annual?), usually with slender stolons; culms slender and wiry; blades mostly 1 mm or less broad; inflorescence branches infrequently as much as 2 cm long ..... 36b. *B. parryi* var. *gentryi*

36a. **Bouteloua parryi** (Fournier) Griffiths var. **parryi**.—FIG. 41.

Chondrosium parryi Fournier, Mex. Pl. Gram. 2: 150. 1886. TYPE: Mexico, San Luis Potosí, "Circa San Luis de Potosí," *Parry & Palmer 943 1/2* (US, holotype).

Bouteloua polystachya (Bentham) Torrey var. *vestita* S. Watson, Proc. Amer. Acad. Arts 18: 177. 1883. TYPE: Mexico, Sierra Madre, 40 mi S of Saltillo, *Palmer 1357* (GH, holotype).

Bouteloua vestita (S. Watson) Scribner in L. Dewey, Contr. U.S. Natl. Herb. 2: 531. 1894.

Tufted *annual*. *Culms* strictly erect or somewhat geniculate-spreading, 20–50 (–60) cm tall. *Sheaths* usually with tufts of long hairs on either side of the collar. *Blades* glabrous or sparsely hispid, flat, mostly 1–2.5 mm broad, the uppermost greatly reduced. *Inflorescence* branches 4–8 (usually 5–6), ca. 2 cm long, with 40–60 closely placed spikelets. *Spikelets* usually with 2 rudimentary florets. *Glumes* unequal, the first greatly reduced, hyaline, usually glabrous, the second 3–3.5 mm long, awned from a narrowly bifid tip, the keel pilose with papilla-based

hairs. *Lemma of the lower floret* ca. 3 mm long, pilose or villous on the lower half, with 3 awns 2–3 mm long. *Lower rudiment* with awns 2–3 mm long, the upper rudiment awnless, minute. *Caryopsis* broadly rounded in the middle and tapering to both ends, ca. 1.5 mm long.

Habitat: On sandy slopes and flats at altitudes to 2,000 m.

Distribution: Southern New Mexico (Dona Ana Co.), Arizona (Cochise, Pima, and Pinal counties), and Mexico (states of Chihuahua, Durango, Guanajuato, México, San Luis Potosí, Sinaloa, and Sonora).

36b. **Bouteloua parryi** (Fournier) Griffiths var. **gentryi** (Gould) Gould, stat. nov. and comb. nov.—Fig. 42.

Bouteloua gentryi Gould, Leafl. W. Bot. 5: 199. 1949. type: Mexico, Sinaloa, Imalá, *H. S. Gentry 5000* (ARIZ, isotype).

Tufted *perennial* (or annual?), usually developing stolons. *Culms* slender, wiry, geniculate and often decumbent below, mostly 10–35 cm long, frequently rooting at the lower nodes, the nodes glabrous or the lowermost densely puberulent. *Blades* short, mostly 0.5–1(–2) mm broad. *Inflorescence* branches (2–)3–6, 1–1.5(–2) cm long, with 25–40 closely placed spikelets. *Second glume* with a short awn from a broad, notched apex.

Habitat: In openings along thorn forest at the lower elevations, from near sea level to 400 m.

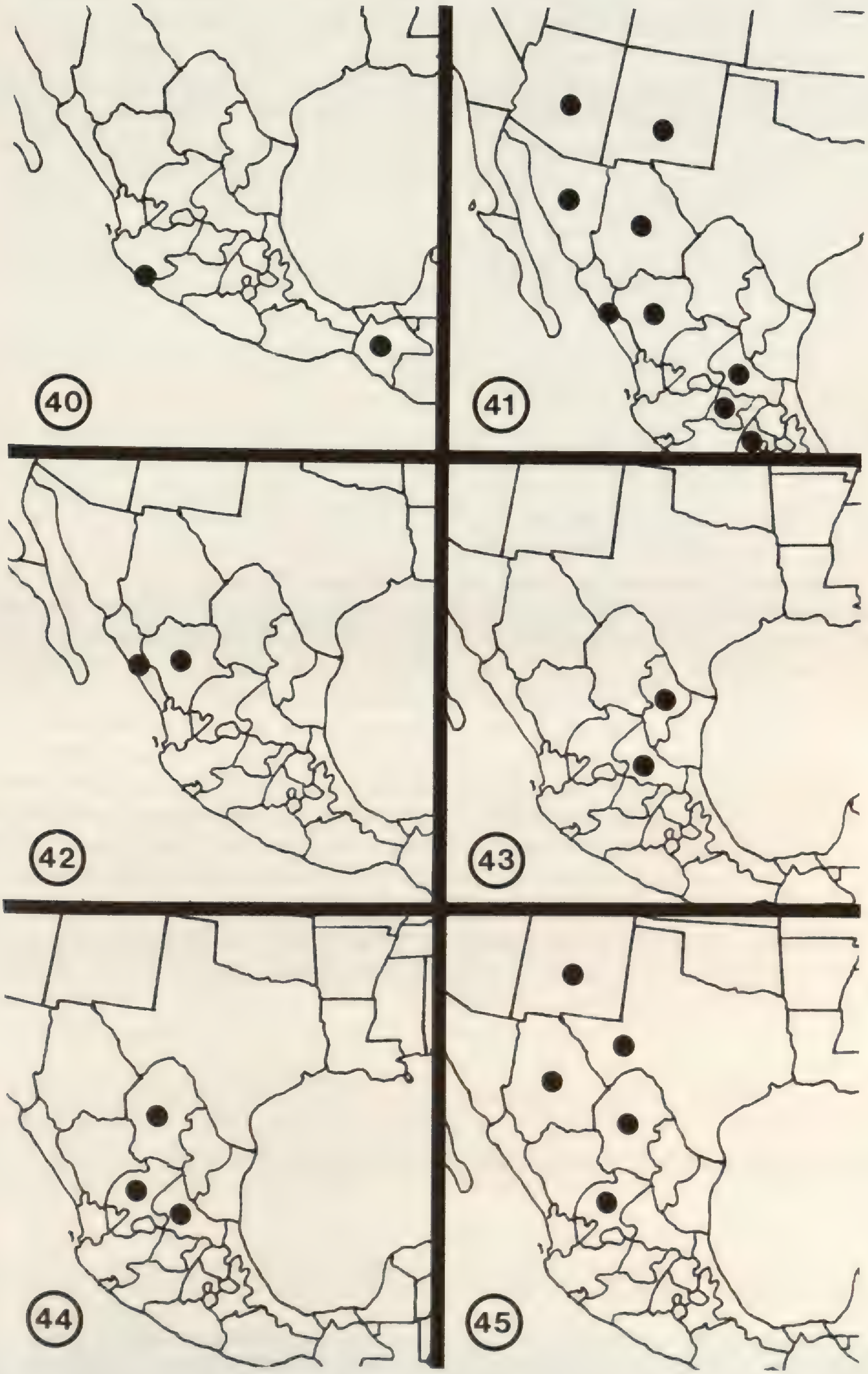
Distribution: Durango and Sinaloa, Mexico, the recorded collections are as follows: Durango: Tamazula, *Gentry 522* (ARIZ), *5244* (GH). Menores and vicinity, in Río Nazas basin, *Gentry 8605* (US). Sinaloa: Cerro Prieta, Culiacán vicinity, *Gentry 7122* (GH, US). 15 mi E of Culiacán, *Reeder & Reeder 2432* (TAES). Mazatlán, *Ortega 4645* (US); *Eyerdam & Beetle 8685* (ARIZ, US). Cerro Llano Redondo, W of Caymanero, *Gentry 7017* (GH, US). Topolobampa, *Rose et al. 13279* (US).

37. **Bouteloua chasei** Swallen, Proc. Biol. Soc. Wash. 56: 81. 1943. type: Mexico, Nuevo León, Galeana, *Chase 7673 1/2* (US, holotype).—Fig. 43.

Tufted *perennial*. *Culms* slender, 20–30(–50) cm tall from a firm or hard rhizomatous base. *Sheaths* shorter than the internodes, more or less puberulent, with a dense tuft of soft hairs to 3 mm long on either side of the ligule. *Ligule* a line of short hairs. *Blades* narrow, involute, flexuous, essentially glabrous. *Inflorescence* branches 3–5, 1.5–2.5 cm long, erect or erect-spreading, persistent. *Spikelets* 3.5–4.5 mm long. *Glumes* more or less puberulent, the first 1.5–2 mm long, the second 3–3.5 mm long. *Lemma of the lower floret* evenly lanate over the back, minutely awn-tipped from a bifid apex. *Rudiment* with a dense tuft of white hairs 1–2 mm long at the base. *Caryopsis* narrowly elliptic, pointed at the basal end, 0.6–0.9 mm long.

Habitat: On dry, gypsiferous soils, often associated with subshrubs.

Distribution: Endemic to southern Coahuila and Nuevo León, and northern San Luis Potosí, Mexico. The following include most of the recorded collections: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Coahuila: 25 mi SW of Monterrey, *Warnock 14820* (K). Between Concepción del Oro and Saltillo, *Almeida et al. 130* (TAES). Nuevo León: 73 mi S of Saltillo, *Gould 10116* (TAES). 4 mi SE of Galeana, *Reeder & Reeder 3966* (TAES). 5 km S of Galeana, *Rojas M. PR-2393* (TAES). 74 mi N of Matehuala, *Waterfall 16591* (US). Galeana, *Hernández & Mathus N-2042* (US); *V. H. Chase 7673 1/2* (US). San Luis Potosí: 84 mi N of San Luis Potosí:, 14 mi N of Hwy. Jct., *Gould 10261* (TAES). 35 mi S of Matehuala, *Gould 10121* (TAES). 46 mi S of Saltillo, *Gould & Watson 10545* (TAE, US). 40 mi S of Matehuala, *Reeder et al. 3298* (TAES, US); *Waterfall 15742* (TAES, US). 2 mi S of Cedral, *Johnston 7592* (US). 36 mi S of Matehuala, *McGregor et al. 542* (US). 5 km S of Matehuala, *Beetle M-382* (TAES). 48 km S of Matehuala, *Roe et al. 70* (TAES).

Bouteloua chasei appears closely related to *B. karwinskii* with which it grows in its restricted area of occurrence. A comparison of these most interesting species has been made by Reeder & Reeder (1963).

38. **Bouteloua karwinskii** (Fournier) Griffiths, Contr. U.S. Natl. Herb. 14: 394. 1912.—FIG. 44.

Chondrosium karwinskii Fournier, Mex. Pl. Gram. 2: 137. 1886. TYPE: Mexico, "Cañon de las Minas et Victoria," *Karwinsky 1479*.

Perennial. Culms slender, erect, 20–30(–50) cm tall from a firm or hard rhizomatous base. *Sheaths* shorter than the internodes, glabrate, ciliate on the margins and with a few long hairs in the throat. *Ligule* a ciliate rim with hair ca. 0.3 mm long. *Blades* flat, 3–9 mm long and 1–2 mm broad, usually scabrous and sparsely pilose on the upper surface. *Inflorescence* branches 3–5, 1–1.8 cm long, spreading or nearly erect; disarticulation apparently at the base of the branch in age. *Spikelets* 3–3.5(–4) mm long. *Glumes* glabrous, the first narrow, acuminate, 1.5–2 mm long, the second broader, acute, 2–2.5 mm long. *Lemma of the lower floret* ca. 3 mm long, sparsely pubescent on the nerves, with an entire, unawned apex. *Lemma of the rudimentary floret* rather deeply cleft, the 3 nerves with awns ca. 1.5 mm long; rachilla glabrous at the base of the rudiment. *Caryopsis* narrowly elliptic or oblong, pointed at the base, ca. 1.6 mm long and 0.3 mm thick.

HABITAT: Known only from gypsiferous or saline sites in Mexico.

DISTRIBUTION: Mexico: Coahuila, San Luis Potosí, and Zacatecas. Records known to me are as follows: Coahuila: 30 mi SW of Monterrey, *Barkley 14727* (K, TAES). 26 mi NNE of Concepción del Oro, *Reeder & Reeder 4000* (US). Near Matrimonio Viejo, *I. Johnston 9370* (US). Western Coahuila, 3–4 mi E of Puerto Caballo, *I. Johnston 8319* (GH, US). S of Laguna de Leche, *I. Johnston 8618* (GH, US). San Luis Potosí: 40 mi NE of San Luis Potosí, *Reeder & Reeder 2926* (TAES). 45 mi NE of San Luis Potosí, *Reeder & Reeder 4077* (TAES, US). Municipio de Guadalcazar, *Rzedowski 8279* (TAES). Municipio Charcas, *J. Villa* in 1973 (DS).

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FIGURES 40–45. Distribution of *Bouteloua* species.—40. *B. elata*.—41. *B. parryi* var. *parryi*.—42. *B. parryi* var. *gentryi*.—43. *B. chasei*.—44. *B. karwinskii*.—45. *B. breviseta*.

39. **Bouteloua breviseta** Vasey, Contr. U.S. Natl. Herb. 1: 58. 1890. TYPE: United States, Texas, Presidio Co., Screw Bean, *Nealley 669* (US, holotype). —FIG. 45.

Bouteloua ramosa Scribner ex Vasey, U.S.D.A. Div. Bot. Bull. 12(1): *pl. 44.* 1890. TYPE: No specimen was cited by Vasey in the original description but Griffiths (1912) agrees with Beal (1896) that the type (neotype) is a Neally specimen from southwestern Texas. *Bouteloua oligostachya* (Nuttall) Torrey ex A. Gray var. *ramosa* (Scribner ex Vasey) Scribner ex Beal, Grasses N. Amer. 2: 418. 1896.

Perennial. Culms clustered from a hard, knotty or subrhizomatous base, wiry, slender, several- to many-noded, freely branching below the middle, mostly 25–70 cm long, the nodes pubescent or glabrous. *Prophylls* of branches densely pubescent with long hairs. *Leaves* inconspicuous, the sheaths shorter than internodes, the blades short and narrow. *Ligule* a minute, hairy collar. *Blades* mostly 1–5(–7) cm long and 0.5–2 mm broad, flat or inrolled. *Inflorescence* branches 1–4 (usually 2), 1–3.5 cm long, densely flowered with 25–45(60) pectinately spreading spikelets, branch rachis mostly 1.5–3.5 mm long, persistent, terminated by a spikelet but this often greatly reduced and needlelike. *Spikelets* with 1 or 2 reduced florets, the rachilla with tufts of long hair at the base of the perfect floret and of the lowermost reduced floret. *Glumes* glabrous or sparsely to densely hairy, with a body 2.5–4 mm long and scabrous awns slightly shorter than the body. *Lower rudiment* with stout awns 3–5 mm long, the upper rudiment, when present, a minute fan-shaped scale. *Caryopsis* obovate, pointed at the basal end, 1–1.2 mm long and ca. 0.4 mm thick.

HABITAT: On dry, rocky slopes, along dry washes in gypsum sands and on calcareous outcrops.

DISTRIBUTION: Texas (Brewster, Culberson, Hudspeth, Kinney, Reeves, and Terrell counties), New Mexico (Chaves, Eddy, and Otero counties), Mexico: Chihuahua: Municipio de Coyame, *Valdez VR718* (TAES). Coahuila: Monclova, *Gould 11191* (TAES). W of Saltillo, *Prat 506* (TAES). S of Castanos, *Reeder & Reeder 3276* (TAES).

Correll & Johnston (1970) recognize *B. ramosa* as distinct from *B. breviseta* although Griffiths (1912), Hitchcock (1935), and Gould (1975) have treated these as synonyms. Beal (1896) distinguished *ramosa* as a variety of *B. breviseta.* Correll & Johnston give the range of *B. breviseta* as Trans-Pecos (Texas) and New Mexico, and the range of *B. ramosa* as Texas and southern New Mexico to Chihuahua, Coahuila, and Zacatecas.

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ERYTHRINA SYMPOSIUM III.[1] *ERYTHRINA* (FABACEAE: FABOIDEAE): INTRODUCTION TO SYMPOSIUM III[2]

PETER H. RAVEN[3]

ABSTRACT

About half of the approximately 110 species of *Erythrina* (Fabaceae: Faboideae), comprising New World species of six sections of subgen. *Erythrina*, are characterized by tubular flowers in which the standard is elongated and the keel and wings are reduced. These species, which are pollinated predominantly by hummingbirds, have relatively low concentrations of amino acids and high sucrose/hexose ratios in their nectar. In the remaining 12 species that occur in the New World and all but two of those of the Old World, the flowers are more or less gaping, with the standard tending to be ovate or obovate and the keel and wings more or less conspicuously exserted. These species are pollinated predominantly by medium-sized passerine birds; their flowers have relatively high concentrations of amino acids and low sucrose/hexose ratios in their nectar. In the two species of the southern African sect. *Humeanae* of subgen. *Erythrina*, the floral morphology resembles that of the New World humingbird-pollinated species. They are pollinated by small sunbirds and white-eyes. Several and perhaps all species of *Erythrina* have a large gland at the apex of the calyx that secretes nectar; ants, attracted to this nectar, patrol the plants and help to protect them from herbivores. A report of short-styled flowers in *E. leptorhiza* is reviewed, and papers providing new information on the taxonomy, alkaloids, modes of propagation, and bruchids of *Erythrina*, included in this symposium, are mentioned.

Most of the papers in the present symposium address the pollination relationships of *Erythrina*, and they add significantly to our body of knowledge concerning this interesting field. The basic division of the genus, from the standpoint of pollination biology, is between those species in which the standard tends to be ovate or obovate, and the keel and wings are more or less conspicuously exserted from the calyx, and those in which the standard is elongated and the keel and wings are reduced. In the first group of species, the corollas are often more or less gaping, the sucrose/hexose ratios are low, and the proportion of amino acids in the nectar is often extremely high. Included here are all species of the genus except some of those of the large subgen. *Erythrina*, and all species of *Erythrina* that occur in the Old World except those of the ditypic southern African sect. *Humeanae* Barneby & Krukoff of subgen. *Erythrina*. In the second group, comprising six related American sections of subgen. *Erythrina* and about half of the species of the genus, together with the two species of sect. *Humeanae* of the same subgenus, the corollas are narrow and tubular. In the American ones, the nectar has high sucrose/hexose ratios, and low proportions of amino acids.

Within the Old World, only *Erythrina zeyheri* Harvey and *E. humeana* Sprengel (sect. *Humeanae*) have relatively narrow corollas that correspond to those of the American species of subgen. *Erythrina* just mentioned. As Jacot

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Guillarmod and her collaborators have shown in this symposium, the Cape white-eye (*Zosterops pallidus*) is the most frequent visitor to the flowers of *E. humeana*, and the malachite sunbird (*Nectarina famosa*) the most important visitor to the flowers of *E. zeyheri*. Sunbirds are likewise frequent at the flowers of the introduced American *E. crista-galli* L., but in the other southern African species of the genus, which have more or less gaping corollas like those of the other species of the Old World, larger passerine birds, such as weavers, starlings, orioles, and bulbuls are the important pollinators, along with the larger sunbirds, whereas white-eyes are insignificant as pollinators.

In general, larger passerines seem to be the most important pollinators of all Old World species of the genus except the two of the southern African section *Humeanae*, and also of the dozen New World species that are not primarily pollinated by hummingbirds. As Corner (1940: 368) has pointed out for the Malayan species, "All the flowers in a whorl are open on the same day. Small birds may therefore drink their fill in a single visit, but they are too light to depress the flowers and reach the style and stamens: only heavy-bodied birds are the effective pollinators." He might have added that only the heavier-bodied birds, in consequence of their nectar requirements, were likely to move from tree to tree and thereby to effect cross-pollination (Heinrich & Raven, 1972). A similar relationship has been outlined well in this symposium for *E. fusca* Loureiro by Morton and by Feinsinger and his collaborators.

In the New World, there are, as summarized by Toledo and Hernández in this symposium, in addition to more than 50 species of subgen. *Erythrina* that have flowers like those of the second group outlined above and which are visited and pollinated by hummingbirds, an additional 12 species that have flowers like those of the first group. These belong to three subgenera, *Erythrina* (3 species), *Micropteryx* (Walpers) J. G. Baker (7 species), and *Erythraster* Barneby & Krukoff (2 species), and include all of the New World species of the two latter subgenera. Papers presented in this symposium and the literature summarized in them indicates that most of the species about which sufficient information is available, *E. fusca*, *E. poeppigiana* (Walpers) O. F. Cook, *E. breviflora* A. DC., and *E. oliviae* Krukoff, are primarily pollinated by orioles and other relatively large passerine birds, but also that they, like Old World species grown in the New World, may also be visited by and pollinated by hummingbirds. In this connection, Morton has presented the fascinating hypothesis in this symposium that the burnt-orange coloration of the apical portion of the wings of *E. fusca* in Panama has evolved there in connection with pollination by male overwintering orchard orioles, which match it in color, and that the comparable spot on the flowers of this pantropical species will be found to differ in color elsewhere. In *E. megistophylla* Diels, which occurs in the lowland tropical wet forests of Ecuador, Steiner has shown that honeycreepers are the principal visitors.

Bats have been observed visiting the flowers of a population of *Erythrina fusca* in Colombia (Helverson in Raven, 1977), but Feinsinger and his coworkers have pointed out that nectar flow in this species, in Trinidad at least, is diurnal, so that pollination by bats is unlikely to be frequent. Arroyo (1980) has suggested that bats may also pollinate the "shaving-brush" flowers of *E. velutina*, but these

flowers are relatively similar to the oriole-pollinated ones of the Mexican *E. oliveae*, described by Toledo and Hernández in this symposium. At any event, bat-pollination has not been shown to be characteristic of any species of *Erythrina*, and the single record probably simply results from opportunistic utilization by the bats of the large amounts of nectar available at the flowers of this genus. Squirrels have likewise been reported feeding at the flowers of *Erythrina* in both the Old World and the New World, and insects have also been reported as occasionally abundant (summaries in Raven, 1974, 1977). In Amazonian Peru, Janson & Terborgh (1979) reported that the flowers of *Erythrina* sp. were an important food source for the monkey *Ateles paniscus*, which however ate and did not pollinate them, in the same area where they observed effective pollination by primates of the flowers of *Ceiba*, *Quararibea*, and *Combretum*. They reported that although icterid birds were probably the normal pollinators of *Erythrina* in the Manu National Park, the monkey and also several species of parrots of the genera *Aratinga* and *Ara* regularly ate the flowers in large quantities. Similarly, Ian Tattersall (pers. comm.) has reported that the flowers of *Erythrina fusca* constitute over half of the diet of *Lemur fulvus mayottensis* in the dry season; the implication is that, as in the case of *Ateles* monkeys in Peru, the flowers were eaten and pollination did not occur. In summary, there is no evidence for nonflying mammals effectively pollinating the flowers of *Erythrina* (summary of this pollination system in Sussman & Raven, 1978) and only one authenticated record of bats making such visits. On the basis of present evidence, it may be concluded that all species of *Erythrina* are bird-pollinated, with about half of the species of the genus, representing all but twelve of the New World species of subgen. *Erythrina*, pollinated primarily by hummingbirds but occasionally also visited by passerines, and the other half, representing all Old World species and a dozen from the New World, primarily pollinated by passerines, mostly relatively large ones, but also visited by hummingbirds when they are native to or cultivated within the area where these birds occur.

The more copious nectars of the passerine-pollinated species of *Erythrina*, which are less concentrated in sugars but much richer in amino acids, both as to quantity and to number of kinds, than those of the hummingbird-pollinated species, seem to provide a food source that is complete or nearly so for their passerine visitors, which have frequently been reported to defend the flowers (Cruden & Hermann-Parker, 1977; this symposium). It may be presumed, as suggested to me by H. G. Baker, that the nectar constituency of the flowers of *Erythrina* species respectively pollinated by hummingbirds and by passerines is related to the fact that the hummingbirds are constantly feeding on insects while they are feeding, the passerines not. The tubular, closed corollas and relatively low concentrations of amino acids in the flowers of hummingbird-pollinated species of *Erythrina* are both apparently specialized features that tend to restrict visits to the flowers of these species by other kinds of birds.

It seems likely, on the basis of present evidence, that the nectars of some species of *Erythrina* are, on the bases of their included phenolics, alkaloids, and other substances, repellent to ants and other nectar-robbers (Baker & Baker, this symposium). Feinsinger & Swarm (1978) have shown that this may be the case

for *E. fusca*, but not for *E. poeppigiana*, and Baker & Baker (this symposium) have suggested that *E. herbacea* L. (hummingbird-pollinated) may have nectar that is less attractive to ants than that of *E. crista-galli* (presumably passerine-pollinated, although visited by hummingbirds). Skead (1967) has implied that the nectar of *E. caffra* Thunberg is more bitter than that of other southern African species he investigated, and Corner (1940: 368) refers to the "somewhat bitter, watery honey" of species of *Erythrina* in Malaysia (pollinated by passerines).

At any event, several of the papers in this symposium have brought back to attention an observation first made by Mattei (1925) on a species of *Erythrina* from Eritrea. In at least several, and perhaps all, species of the genus, there is at the summit of the calyx a large nectary. This extrafloral nectary secretes copious nectar, which attracts ants, and the ants that are attracted patrol the plant and protect it from many kinds of insect herbivores, in the mode outlined by Bentley (1977) for many different kinds of tropical and extratropical plants. This phenomenon should be studied throughout the genus to see if it is ubiquitous, and it would be of interest to see what kinds of relationships occur on some of the distant oceanic islands that *Erythrina* species with buoyant seeds have colonized. It might be that the heavy infestations of the Bucare twig borer, *Terastia meticulosalis*, that makes the cultivation of *Erythrina* in southern Florida almost impossible (Raven, 1974) are related to an absence of the normal protective ant fauna, either naturally or as a result of the application of pesticides, and the relationship might be important with respect to the success of the genus in cultivation. The chemical constituency of the nectars in the floral and extrafloral nectaries of *Erythrina* should be compared, especially in a species such as *E. fusca* that has been shown to have floral nectar that is somewhat distasteful to ants (Feinsinger & Swarm, 1978). Sherbrooke & Scheerens (this symposium) have already presented evidence that the high sucrose/glucose ratio in the floral nectar of this species is much lower in the extrafloral nectaries, both calycine and foliar. Feinsinger et al. (this symposium) have pointed out that while ants are characteristically abundant around the outside of the flowers of *Erythrina*, they are very rarely found within; and the reasons for this relationship would be of great interest. In addition to the large gland on the calyx, Sherbrooke & Scheerens (this symposium) have called attention to the foliar nectaries in *E. flabelliformis* Kearney, the presence of which in other species of the genus ought also to be investigated. Once again it is emphasized that a genus such as *Erythrina*, for which a great deal of chemical information is available, is an ideal subject for the investigation of predator-prey relationships and coevolution.

A final major point concerning pollination systems that has been brought out in this symposium is the observation of Hernández & Toledo that *Erythrina leptorhiza* A. DC. forms some flowers with short styles that also differ in other characteristics from the normal ones. Hernández and Toledo have reported that about 20% of the flowers they examined had short styles, shorter than the anthers; they did not obtain any seed set following the self-pollination of either kind of flower. The apparently very interesting breeding system of this species should be investigated in more detail.

In addition to the papers just reviewed, which present a great deal of new information on pollination relationships and other plant-animal interactions involving *Erythrina*, this symposium also includes a new review of the taxonomy of the genus by B. A. Krukoff, providing an updated report upon the basic classification system and the new discoveries that have been made during the past three years. The taxonomy of the bruchid *Specularius impressithorax*, the only known bruchid that attacks the seeds of *Erythrina*, with their alkaloids and nonprotein amino acids, is reviewed. Information on the alkaloid constituency of the seeds of a further 14 species of *Erythrina* is presented by A. H. Jackson and his collaborators, thus adding to the rich store of information on *Erythrina* alkaloids and helping to provide a basis for further biological investigations. In addition, Keith Woolliams has provided a useful digest of culture methods in *Erythrina*, based mainly upon his experiences in Hawaii. No further biosystematic information is presented, but the living collections—and particularly that at the Pacific Tropical Botanical Garden in Kauai—continue to grow, so that we may soon have ample and reliable information on the patterns of self- and intercompatibility in this widespread and fascinating genus.

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NOTES ON THE SPECIES OF *ERYTHRINA*. XII

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Abstract

Based on an examination of 377 new collections, range extensions are noted for 24 species, *Erythrina sousae* Krukoff and *E. lanata* subsp. *calvesces* Krukoff are newly described, *E. megistophylla* is reinstated as a valid species, two forms (*E. petraea* and *E. oaxacana*) are raised to specific rank, and *E. crista-galli* var. *corallina* is reduced to synonymy. All new specimens from Nicaragua are cited, as well as selected African and Asian specimens. Vouchers are cited for specimens used in the chemical and pollination studies reported in this symposium.

Other papers in this series "Notes on the species of *Erythrina*" have been published as follows: Suppl. X (Krukoff, 1977b), Suppl. XI (Krukoff, 1978), Suppl. XIII (Krukoff, 1979a), Suppl. XIV (Krukoff, 1979b).

In connection with the preparation of this paper 377 new collections were examined. Of particular interest are the enormous new collections made in Mexico by the new head of National Herbarium, Mario Sousa, and his collaborators. Of 28 species and subspecies of *Erythrina* which occur in Mexico, only six (*E. petraea*, *E. montana*, *E. pudica*, *E. tuxtlana*, *E. tajumalcences*, and *E. berenices*) are not represented in this collection. Of particular interest are the new species, *E. sousae*, the first collection of *E. oliviae* outside of the type locality and the first collection since 1939 of *E. oaxacana*, which permitted the raising to specific rank of two forms (*E. breviflora* f. *petraea* and *E. breviflora* f. *oaxacana*).

Recent establishment of Río Palenque Science Center in the province of Los Ríos, Ecuador permitted me to receive for the first time fruits of *E. megistophylla*, which is very common in this region, resulting in its reinstatement as a valid species. It should be kept in mind that fruiting collections of *E. edulis* and its relatives are exceedingly rare, largely because of difficulties in preserving the easily spoiled, large, soft, and succulent seeds. *Erythrina megistophylla* seems to be confined to a narrow strip of low altitude wet forest along the western base of the Andes.

In connection with the project of the Flora of Nicaragua, now underway, I am citing in this paper all new collections from this poorly collected country. Vouchers for seeds under chemical studies by Prof. Jackson, specimens of *Erythrina* which were studied in relation to pollination, as well as collections of some selected African and Asian species which are of special interest, are also cited herein.

After 8 years of efforts we are now approaching the aim which we set before ourselves back in 1968 when I started extensive collections of *Erythrina* seeds in Central America. Between the Pacific Tropical Botanical Garden and Waimea Arboretum in Hawaii, we are growing around 70 species most of which were in flower in March 1979. I went there recently to lay the ground work for Dr.

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Herbert G. Baker (Berkeley) to study the constituents of their nectar in March 1980, and for genetic work which was initiated by Dr. W. L. Theobald in 1979. Incidentally, as a by-product of genetic studies we eventually hope to find some handsome hybrids resistant to drought, which would be very desirable for Hawaii, and some hybrids tolerant to frost, which would be desirable for cultivation in California. The living collection of *Erythrina* is in two compact, easily accessible areas, and as the trees are still young, their flowers can be reached by hand, an ideal condition for this type of work.

Erythrina Symposium IV is now being organized to be published late in 1980. It likely will include among others, papers on constituents of nectar of various species by Herbert G. Baker, on wood anatomy by Baretta-Kuiper (Utrecht), on erythrinas cultivated in California by Elizabeth McClintock, on minor alkaloids of erythrinas by A. H. Jackson, and the first paper on the genetics of the genus.

In the citation of specimens in this paper, those not followed by a herbarium acronym are deposited in the herbarium of the New York Botanical Garden (NY).

1. *Erythrina fusca* Loureiro, Fl. Cochinch. 427. 1790, based on *Gelala aquatica* Rumphius, Herb. Amb. 2: 235. *tab.* 78. 1750.

Nicaragua: *Avinoan Danin 76-22-2* (N of San Pedro); Matagalpa: roadside, ± 530 m, *W. D. Stevens 6033* (MO); Rivas: *W. D. Stevens 6624, 6639* (Isla de Ometepe), *William T. Gillis 10280* (F). Comores: Mayotte, *Tattersall 1* (K), *2* (K), *3* (K).

2. *Erythrina crista-galli* L., Mant. 99. 1767.

Erythrina crista-galli L. var. *corallina* N. Mattos, Loefgrenia 71: 3. 1977.

I have not seen the holotype of the variety [*J. Mattos 17372* (IPRN)] which is from a cultivated tree growing at Parque Farroupilha, Pôrto Alegre, Rio Grande do Sul. There is nothing in the description to suggest that it should be considered as a good variety.

Erythrina crista-galli has been widely cultivated from very early times, and is known at present in North America, and in many countries in South America, Africa, Asia, and Australia. As a consequence, there are many horticultural forms and hybrids.

Mexico: Distr. Fed.: Jard. del Pedrigal, cult., *H. Hernández 3* (Aug. 12, 1978).

3. *Erythrina falcata* Bentham in Mart., Fl. Bras. 15(1): 172. 1859.

Brazil: Mato Grosso: on road to Xavantina, *J. A. Ratter 2242* (UB).

This is the first record of this species from Mato Grosso.

4. *Erythrina dominguezii.* Hassler, Physis 6: 123. 1922.

Below is quoted a letter of Augusto G. Schulz, an eminent student of the Flora of Chacó, providing an elegant description of flowering and fruiting of this species:

Este hermoso árbol está actualmente (Mayo 20) con las ramas desnudas sin una hoja. Por setiembre–octubre se vestirá de gala con sus flores rosadas y ya pasada la floración vendrán las

hojas nuevas. Por diciembre, más o menos, estarán maduras las legumbres, con 2 a 4 semillas. Es una vaina ancha papirácea, que se abre sobre el árbol sin largar los granos; la llevara el viento pues es muy voladora. De modo que las semillas deben ser juntadas en el suelo, en las proximidades del árbol, según et viento.

The ranges of *E. dominguezii* and *E. verna* are partly in regions poorly accessible at the present time, and, at least in Mato Grosso and the Federal District in Brazil, their ranges seem to overlap. Furthermore, they are leafless when in flower and, as a result, many specimens are incomplete. It would be important to define more clearly their ranges of distribution. These two species can be distinguished in the field by color of the flowers: pink (rosadas) in *E. dominguezii* and red (rojas) in *E. verna*.

Argentina: Chacó: Colonia Benítez, *A. G. Schulz s.n.* (22/12-1978).

This is a voucher for the seeds which are under chemical studies by Prof. Jackson.

6. *Erythrina verna* Velloso, Fl. Flum. 304. 1825.

Brazil: Minas Gerais: *V. Gomes 2809A* (UB), *E. P. Heringer 2809B* (UB) (Fazenda São Clemente, cult.), *E. P. Heringer 7603* (UB) (Paraopeba); Distr. Fed.: Brasilia, *E. P. Heringer 16978* (RB) (na margem do cerrado).

Trees cultivated at Fazenda São Clemente have "white flowers." *Heringer 16978* is the first record of this species from the Federal District.

7. *Erythrina poeppigiana* (Walpers) O. F. Cook, U.S.D.A. Div. Bot. Bull. 25: 57. 1901.

Nicaragua: sierras de Managua (cult.), *David Neill 1075.* Brazil: Rondônia: Rio Pacaás Novos, *N. A. Rosa 887, W. Rodrigues 9645* (INPA).

This is the first record of this species from Rondônia.

8. *Erythrina suberosa* Roxburgh, Hort. Beng. 53. nomen 1814; Fl. Ind. 3: 253. 1832.

India: Bangalore: Pondichery, *G. Thanikaimoni 1301.*

This is a voucher for seeds which are under chemical studies by Prof. Jackson.

9. *Erythrina microcarpa* Koorders & Valeton, Booms. van Java 2: 61. 1895.

Java: *Herb. Bogor 9620* (BO), *12785* (flrs.) (L), *14598* (flrs. & young frts.) (L), *14599* (flrs.) (L), *Herb. Koorders. 46* (sterile) (L), *49* (sterile) (L), *51* (sterile) (L), *65* (flrs.) (L), *66* (frts.) (L), *71* (flrs.) (L), *72* (flrs.) (L), *coll. undesign. s.n.* (30/9-1931) (BO). Timor: *Herb. Bogor 50* (BO).

Outside the herbaria in Leiden and Bogor, this species is very poorly represented in collections and my recent search for it in various herbaria in the Orient and Europe was unsuccessful.

The species is confined to eastern Java and probably the neighboring Madura and Bali. I found a specimen of it from Timor among the unidentified specimens on the recent visit to the Bogor Herbarium.

10. *Erythrina stricta* Roxburgh, Hort. Beng. 53, nomen 1814; Fl. Ind. 3: 251. 1832.

India: *G. Ghose & Co. s.n.* (1978) (Darjeeling), *G. Thanikaimoni 1329* (Yercaud).

These two specimens are vouchers for seeds which are under chemical studies by Prof. Jackson.

11. *Erythrina resupinata* Roxburgh, Hort. Beng. 53. nomen 1814; Pl. Coromandel 3: 15, *pl. 220.* 1819.

The name of this species suggests that flowers are deflected from the rachis downward, as is the case with *E. folkersii*, *E. humeana*, and certain other species. It will be interesting to study pollination of it, which will be possible when our plants in the Waimea Arboretum, Hawaii come of age.

13. *Erythrina subumbrans* (Hasskarl) Merrill, Philipp. J. Sci. 5: 113. 1910.

India: *G. Thanikaimoni 1328* (Yercaud); Karnatak (=Mysore): Chickenalli, 900 m, *A. Meebold 9728* (Holotype of *E. mysorensis* Gamble) (CA).

Thanikaimoni's specimen is a voucher for seeds which are under chemical studies by Prof. Jackson.

14. *Erythrina breviflora* Alph. DeCandolle, Prodr. 2: 413. 1825.

I have treated (Krukoff, 1939) three perennial herbs, *E. leptorhiza*, *E. horrida* and *E. montana*, native to Mexico and closely related, as distinct species as they are well collected and understood. *Erythrina leptorhiza* is known from 109 collections from ten states, *E. montana* from 26 collections from five states, and *E. horrida* from 18 collections from the state of Oaxaca, and their ranges do not overlap. For their differences see the key in Krukoff & Barneby (1974: 363).

I (Krukoff, 1939) treated three small shrubs native to Mexico and closely related, as a single species, *E. breviflora* and two forms. Their ranges do not overlap but they are poorly collected, as related under *E. patraea* and *E. oaxacana*. I thought that the specimens were perhaps collected from the upper portions of plants and that the leaflets naturally were much smaller than those of the average collections of *E. breviflora*. The new collection by Mario Sousa of *E. oaxacana* is not only the first collection of the two entities since 1939, until now treated by me as forms, but provides the irrefutable evidence that the leaflets are normal and not confined merely to the upper portion of the plants. I now raise them to the rank of species. For their differences see Krukoff & Barneby (1974: 358).

14a. *Erythrina petraea* Brandegee, Zoe 5: 247. 1908.

Erythrina breviflora f. *petraea* (Brandegee) Krukoff, Brittonia 3: 255. 1939.

Mexico: Puebla: *C. A. Purpus 2680* (UC—holotype, DS).

For the reasons why I again have raised this entity to specific rank, see under

E. breviflora. It is still known only from five collections by C. A. Purpus from Cerro de la Yerba and one from Sierra de Mixteca, all in the state of Puebla and cited in my first monograph (Krukoff, 1939: 255).

14b. *Erythrina oaxacana* (Krukoff) Krukoff, comb. nov.

Erythrina breviflora Alph. DeCandolle f. *oaxacana* Krukoff, Brittonia 3: 256. 1939.

Mexico: Oaxaca: Mitla, ± 1833 m, *L. C. Smith 109* (US—holotype); Distr. Tlaculula, 8 km to the N of Díaz Ordaz (road to Guajimalaya), ± 2050 m, *Mario Sousa 7807.*

I have been waiting for a new collection of this entity since 1939; it was previously known only from three collections (including the type), all from high elevations in the state of Oaxaca.

Seeds of this species were collected for the first time (*Mario Sousa 7807*) and are described here: seed black, ±18 mm long, ±11 mm broad, hilum round, grayish ±2 mm in diam.

15. *Erythrina edulis* Triana in M. Micheli, J. Bot. (Morot) 6: 145. 1892.

Panama: Chiriquí: *K. E. Blum 2530A* (July 24, 1966—frts.) (SCZ), finca Collins, vicin. Boquete, cult.; *Grady Webster 16663* (June 21, 1971—flrs. scarlet), distr. Boquete, above Jaramillo, along N. slopes of Cerro Palo Alto, disturbed rain forest, ± 1333 m; *Laurence E. Skog 4062* (March 21, 1977—flrs.) (MO) coffee plantation near Boquete, ± 1400 m; *J. P. Folsom 2229* (flrs. orange red) (MO), cult. as a shade for coffee, *Barry Hammel 3017* (MO) (lower north slope of Barú, forest edge and pasture, 6000–6500 ft). Colombia: Cundinamarca: *H. García-Barriga 20059, 20062.* Ecuador: Napo-Pastaza: *H. Balslev Madsen 10324* (AAU) (Baeza, 2000–2200 m), *E. W. Davis 347* (S) (near Cosanga), Tungurahua: ± 1800 m (Aug. 13—frts.).

Specimens of E. edulis *seen by me in April 1979.*—In connection with the reinstatement of *E. megistophylla* as a valid species it is desirable to reexamine numerous (±200) specimens of *E. edulis* to ascertain which, if any, should be transferred to *E. megistophylla.* This I plan to do on my trips to various herbaria, but in the meantime I reexamined specimens which are deposited at NY, and they are cited below to facilitate the checking of other collections.

Venezuela: Táchira: *Steyermark 101274.*

Colombia: Antioquia: *Toro 834, 1082, Robledo s.n.* (*Kr. Herb. 15158*); Boyaca: *Lawrance 285, Ramos Nuñez s.n.* (*Kr. Herb. 15190*), *Pennell 8681*; Cauca: *Pennell & Killip 8047, 8288, Ramos Nuñez s.n.* (*Kr. Herb. 9413*); Cundinamarca: *Karsten s.n., Jaramillo s.n.* (*Kr. Herb. 9182*), *E. L. Little Jr. 7421, García-Barriga 12414, 17517, 20112, Al. Gentry 17129*; Huila: *Rusby 952.* (Total 17 collections.)

Peru: *Ocampo s.n.* (*Kr. Herb. 9530*); Amazonas: *Jef. D. Boeke 2084, Hutchinson 6831*; Cajamarca: *Woytkowski 6972*; Ayacucho: *Killip 22827*; Huánuco: *J. Schunke 8313*; Junín: *Killip 25840*; Pasco: *Woytkowski 7354.* (Total 8 collections.)

Ecuador: Azuay: *Camp E-537, E-2198, E-4403, MacBryde 446, 454*; Chimborazo: *Ira L. Wiggins 11061*; Loja: *Asplund 18033, Reinaldo Espinosa 668, 1347, Harling 6040, Hitchcock 21340, MacBryde 645, Penland 1152, Wiggins 10883*; Napo-Pastaza: *Jef. D. Boeke 378, C. H. Dodson 1960, MacBryde 848, 1493, P. J. M. Maas 3049* (U); Morona-Santiago: *Alberto T. Ortega U. 207*; Pichincha: *Asplund 16705*; Tungurahua: *MacBryde 665.* (Total 22 collections.)

Bolivia: La Paz: (?) *Buchtien s.n.* (*US 1097832*).

Specimens of E. edulis *not seen by me in April 1979.*—From the card file of specimens of *E. edulis* seen by me since 1939, I compiled statistical data on specimens which were *not* seen by me in April 1979. Inasmuch as very few of

these, if any, are of *E. megistophylla*, these data give a fairly accurate distribution of *E. edulis*.

Colombia: Dept. undesign.—4 specimens; Antioquia—9; Caldas—1; Cauca—12; Cundinamarca—10; Huila—3; Magdalena—1; Norte de Santander—1; Putumayo—3; Tolima—4. Total—48 collections. Peru: Dept. undesign.—5; Amazonas—2; Ancash—2; Apurimac—2; Ayacucho—2; Cajamarca—2; Cuzco—6; Huánuco—3; Loreto—1; Pasco—1. Total—26 collections. Ecuador: Prov. undesign.—6; Azuay—1; Bolívar—2; Cañar—1; Chimborazo—6; Cotopaxi—2; El Oro—1; Esmeraldas—1; Imbabura—1; Loja—8; Los Ríos—2; Pichincha—5; Tungurahua—7. Total—44 collections.

Erythrina edulis *in Panama*.—In Suppl. VII I (Krukoff & Barneby, 1973: 110) cited the first collection of this species from Chiriquí, Panama, probably from a cultivated plant [*Croat 10629* (MO)]. In Suppl. VIII (Krukoff, 1976: 345) the second collection from a coffee plantation was cited [*M. Nee 10624* (MO)]. Five additional collections are cited in this paper. All of these collections are of *E. edulis* probably introduced to Chiriquí as a shade for coffee. *Webster 1663* has inflorescences borne on the old wood.

It would be important first to determine, presumably from finca Collins and/or other neighboring fincas, the source of their *E. edulis*, and secondly to procure seeds of the two forms, one with the more common type of inflorescence and the other with cauliflorous ones, for genetic studies in Hawaii.

Cauliflorous inflorescences are rarely found in species of *Erythrina*. They occur invariably in *E. megistophylla*, very seldom in *E. edulis*, and recently I received an excellent specimen of *E. schimpffii* [*Plowman 5457*, wrongly cited in Suppl. IX (Krukoff, 1977a) as "*3457*"] accompanied by excellent photos (presently filed at NY) which show inflorescences borne on the old wood.

Erythrina edulis is a medium size tree with orange flowers (standards), as is also the case with its close relative, *E. megistophylla*. It has a very extended distribution and thrives under more diversified altitudinal conditions than any other species of the genus. It has been cultivated extensively from times immemorial throughout the area to which it is native, and this must have added to its present complexity. The species is fairly uniform, by "*Erythrina* standards," in its vegetative and floral characters, both in the northern (Colombia) and in the southern (Peru) portions of its range, but is much more complex in Ecuador, which is also the home of *E. megistophylla*, *E. polychaeta*, and *E. schimpffii*, its only close relatives.

Unlike *E. megistophylla*, which is *usually* found at elevations below 300 m, *E. edulis* is *usually* found at elevations between 1,250 and 2,750 m. However, it occasionally occurs at much lower elevations, e.g., *Alberto T. Ortega U. 207* from the province of Morona-Santiago and *Acosta-Solis 13957* from Chimborazo are from an elevation of 300 m.

Below I will discuss very briefly some of the specimens which exhibit characters unusual for the species: *Killip 25840* (NY, US) (Junín, Peru) with inflorescences borne at the base of the trunk; *Camp E-4403* (Azuay, Ecuador) with inflorescences on the larger branches and trunk, in the manner of *E. megistophylla* and sometimes of *E. schimpffii*; *García-Barriga 12414* (COL) (Cundinamarca, Colombia) with small spines on the petioles and on the secondary veins on the upper surface of the leaflets, in this respect resembling *E. polychaeta*, and

Elbert L. Little Jr. 7421 (Cundinamarca, Colombia), *Schunke 8313* (Huánuco, Peru) and *Felix Woytkowski 7354* (Pasco, Peru) with small spines on the petioles.

As might be expected, the flowering season of this species varies considerably in different altitudes, localities, and regions.

For better understanding of the group, it will be necessary to introduce *E. edulis* and its relatives to Hawaii and study them genetically.

15a. *Erythrina* aff. *edulis* Triana

This *Erythrina* cannot be fully understood in the absence of fruits. It is characterized by a striking reticulation pattern of the leaflet blades, which is sharply elevated on the faces of the leaflets. For convenience, I am citing below all these specimens deposited with NY which I examined recently.

Ecuador: Chimborazo: 5.6 km W of Pallatanga, *MacBryde 694* (flrs.—Sept. 4, 1971); Cotopaxi: Pilalú, ± 2320 m, *MacBryde 561* (flrs.—July 7, 1971); Tungurahua: ± 1900 m, *Penland 101* (flrs.—March 16, 1939); Napo-Pastaza: *Harling 3921* (flrs.—Jan. 26, 1959), *B. MacBryde 860* (just W of Baeza, ± 1960 m) (flrs.—Oct. 26, 1971), *863* (1 km WNW of Cuyujúa, ± 2500 m) (flrs.—Oct. 27, 1971), *J. D. Dwyer 9588* (vicin. Baeza, ± 1900 m) (flrs.—March 27, 1972), *Al. Gentry 12407* (± 2800 m) (flrs.—Nov. 4, 1974).

This *Erythrina* is a tree, up to 8 m, from high elevations (1,900–2,800 m).

I am now trying to obtain its fruits which possibly will help to understand it better. In addition, it is desirable to introduce it to Hawaii for genetic studies. Dr. Russel J. Seibert, formerly at MO, referred to these specimens as "grading into *E. polychaeta*."

T. Plowman 3923 from Napo, canton Quijos, ±2,133 m, is important as it is the first collection seen which "grades" from the common *E. edulis* to this entity.

Rupert Barneby opened two flowers (*Al. Gentry 12407* and *B. MacBryde 561*) and found 8 and 10 ovules.

15b. *Erythrina megistophylla* Diels, Biblioth. Bot. 116: 96. 1937.

Were it not for the Río Palenque Science Center, established in the early seventies in the province of Los Ríos, Ecuador, this species would probably still be concealed in the synonymy of *E. edulis*. Seeds of *E. megistophylla* and its close relatives are soft, large, and quickly spoiled. Up to Oct. 2, 1976, when *C. H. Dodson 6241* was collected, it was not known that the pods are subspherical and 1-seeded. Only recently I finally received sufficient material, including fruits preserved in alcohol, to justify careful studies of this entity. As happened often in the past nine years, Rupert Barneby provided the important proof that it is a distinct species. He opened several flowers (*Dodson 7333*, *Cazalet 5030*, etc.) and found only a single ovule in each. This means, of course, that there is a really fundamental difference in the fruit and that it is not a simple ontogenetic modification of *E. edulis*.

Ecuador: Guayas: Tafalla (?)—*F. H. D. 267*. L. 558 (photo of B sheet lost in world war—holotype), BM (isotype ?), *A. S. Hitchcock 20417** (GH, NY, US) (Teresita, 3 km W of Bucay, 2/0 m) (flrs., infl. with one very immature 1-seeded fruit—July 5–7, 1923),

* Collections marked with asterisk are cited as *E. edulis* in the list of exsiccatae, Suppl. XIII (Krukoff, 1979a).

*F. Fagerlind 657** (S, NY) (NE of Quillallpa, 150 m) (two leaflets, and one detached infl. with flrs.—Oct. 1952), *W. H. Camp E-3643** (NY) (junction of the provinces Guayas, Cañar, Chimborazo, and Bolívar, foothills of the western cordillera near the village of Bucay, 1000–1250 ft) (lvs. and infl.—June 8–15, 1945) (field label reads in part—inflorescences 1–2 at place, on wood of trunk and older branches, arching downward); Los Ríos: *Carlos Játiva 89** (CAS) (along Río Cristal, ± 70 m) (flrs.—July 1962), general region of Río Palenque Science Center, elev. 150–220 m, *C. H. Dodson 4319* (SEL) (flrs.—Aug. 8, 1972), *5334* (SEL, MO) (flrs.—Sept. 16, 1973), *6241** (SEL, MO) (flrs.—Oct. 2, 1976) (frts. said to be subspherical), *6737** (SEL, MO) (mature well-preserved dry fruit—Aug. 11, 1977), *7333* (SEL, NY) (flrs., and 1-seeded fruit, 10 cm long and 7 cm in diam.—Dec. 1, 1978) (infl. seemed to be elongating for more than one year), *7740* (SEL) (seedling 1 m high with fruit still attached), *Al Gentry 9650* (MO) (flrs.—Feb. 5, 1974), *Thomas B. Croat 38658** (MO), *38702** (MO); Chimborazo: Huigra, *J. N. Rose 22594** (NY, GH, US) (lflts., flrs.—Sept. 8, 1918); Pichincha: *P. C. D. Cazalet 5030** (NY, US, K) (20 km W of Santo Domingo de los Colorados, 1000 ft.) (lvs., flrs.—Oct. 16, 1961), *Carlos Játiva 559** (San Miguel near Santo Domingo, 300–400 m), *Elbert L. Little Jr. 6194* (MAD) (between Santo Domingo to Quininda) (flrs.—Apr. 7, 1943); El Oro: 7.3 mi este de Saracay, 1200 ft., zona de transicion entre bosque seco y el de neblina, *Linda Albert de Escobar 860* (lvs., infl. with flrs.—Nov. 23–Dec. 18, 1978) (fruit is said to be with only one seed).

The type collection of E. megistophylla *Diels.*—At the time I was working on my first monograph of the American species of *Erythrina* (Krukoff, 1939), I had on loan three sheets, two from B and one from BM, which were photographed at NY. The first two sheets were lost during World War II. One sheet from B with a very large single detached leaflet was labelled in Diels's handwriting "*Erythrina megistophylla* Diels, Ecuador, Guayaquil, Tafalla" (Tafalla, of course, was an artist who accompanied Ruiz and Pavón); another sheet had two detached inflorescences and a carefully mounted dissected flower on the right (standard, keel, wings, calyx and stamens with pistil). It also was labelled in Diels's handwriting "*Erythrina megistophylla* Diels, Ecuador, Guayaquil 1800 —Tafalla" and in another hand: "Herbarium Peruanum Ruiz et Pavón, *Erythrina ovata* sp. nov., Vulgo "Zapote de perro," F.H.D. 267, L. 538, Año de 1800." The BM sheet had a very large single detached leaflet and a single detached inflorescence. There is no indication that Diels saw this sheet. In a left corner of the sheet was written in Pavón's handwriting (!) "*Erythrina ovata* sp. nov., Hualgayoc del Peru" (Hualgayoc is in Dept. of Cajamarca, Peru, near 79°W, 7°S).

In the original description of this species Diels states: "West-Ecuador: Prov. Guayas: Guayaquil, 1800, vulgo. "Zapote de Perro." (Tafalla?) *F. H. D. 267.* L. 538"—Typus specie!)."

In my first monograph (Krukoff, 1939) I repeated Diels's statement and wrote: "Tafalla (?) *F. H. D. 267* L. 538" (B, type of *E. megistophylla*, BM)." Diels's specimens naturally were placed by me in synonymy under *E. edulis* Triana as, in addition to Tafalla's specimens, I had seen of this species only *A. C. Hitchcock 20417* (GH, NY, US), which I now recognize as of *E. megistophylla.* The latter was collected in Guayas, Terezita, alt. 270 m on July 2–7, 1923, and has a detached flower with an *immature* 1-seeded pod and very large leaflets.

Although the leaflets and inflorescences on the B and BM sheets are so much alike that they might be from a single branch, we have no irrefutable evidence that they represent a single collection, and, therefore, the BM sheet cannot be considered as an isotype of *E. megistophylla.*

The puzzling question is where Diels obtained information that B sheets

were from Ecuador and not from Peru as written on the same sheets on Ruiz and Pavón's label. Eventually, it may be possible to clarify this by examining Ruiz and Pavón's collections in Madrid, Geneva, Paris, and the British Museum. There are three additional sheets of Pavón's collections in BM and one in P (of the *E. edulis* complex). However, it is merely speculation and in the meantime I have no other choice but to, again, accept Diels's statement in reference to the type locality. Being a careful taxonomist, he must have had reasons for it. I also do not know what F. H. D. and L. stand for. Of course, although we are not certain as to the locality of the type collection, there is no question as to its identity.

Field description.—Nineteen collections of this species are presently available to me, and, as a result, I can make some general statements: it is a rather small spiny tree, usually 3–8 m tall; its flowers (standards) are orange; its inflorescences are invariably cauliflorous, borne on wood of the trunk and older branches, arching downward; its fruits are 1-seeded, subspherical, about 10 × 8 cm when fresh. It occurs at elevations of 70–1,000 m, often in the understory of virgin or secondary forests; it usually is in flower in July or August and has mature fruits from August to October.

Distribution.—Widely distributed in Ecuador and so far collected in the provinces of Guayas, Los Ríos, Chimborazo, Pichincha and El Oro. The remark on the label of *W. H. Camp E-3643* quoted above seems to indicate that it is also found in Cañar and Bolívar.

How it differs from its relatives.—*Erythrina megistophylla* is related to *E. edulis* and less so to *E. schimpffii* and *E. polychaeta*; the last two species are endemic to Ecuador, whereas the first is found in other sub-Andean countries of South America (see under *E. edulis*).

If fruits are present, *E. megistophylla* is immediately recognized since its fruits are unique: subspherical and 1-seeded (pods and seeds of *E. polychaeta* and *E.* aff. *edulis* are not known, but the leaflets of these two species are either regularly setose-aculeate or at least strikingly reticulate on both surfaces).

Flowers of *E. edulis* cannot be distinguished from those of *E. megistophylla* and of *E.* aff. *edulis* as they all have a broad standard about half as wide as long. The standards of *E. schimpffii* and *E. polychaeta* are narrowly elliptic (over twice longer than wide). Incidentally, during my work on the genus in 1939, flower parts (calyces, standards, keel petals, and wings) were mounted on mica slides permitting their examination without making new disections. These are now at NY (15 slides of collections of *E. edulis* from Ecuador, 11 slides from Colombia, and 8 slides from Peru, also 3 slides of *E. megistophylla*).

Leaflets of *E. megistophylla* can be immediately told from *E. polychaeta* as they are not regularly setose-aculeate on both sides, but cannot be distinguished from races of *E. edulis* with large leaflets which occur at low elevations. However, if a specimen is from an elevation less than 300 m and if it also has terminal leaflets broader than long, with nearly truncate bases and 9–10 secondaries, then chances are good that it is of *E. megistophylla.* Sterile specimens with small leaflets (with acuminate apices) are, of course, immediately recognizable as *E. edulis.*

Erythrina lorenoi F. Macbride was described 7 years earlier than *E. megistophylla* with emphasis on the very large, subrotund, nearly square-based leaflets.

Mature leaflets of *E. edulis*, *E.* aff. *edulis*, and *E. megistophylla* are not ceriferous (mature leaflets of *E. polychaeta* were not seen), whereas those of *E. schimpffii* are reticulate-ceriferous beneath. Unfortunately, very few collections have *mature* leaves since the flowers and leaves are contemporary.

Terminal leaflets of *E. megistophylla* are up to 38 cm long and 44 cm broad, petioles up to 66 cm long, secondaries usually 9–10 per side (versus 8 in *E. edulis*). Dried fruit ±7.5 × 4.5 cm, dark brown, pericarp 1.5 mm thick, seed ±2.5 cm long.

16. *Erythrina speciosa* Andrews, Bot. Repos. 7: *pl. 443*. 1806.

Brazil: Distr. Fed.: Brasilia, *E. P. Heringer s.n.* (13/6-1974) (UB).

This is the first record of this species from the Federal District.

17. *Erythrina polychaeta* Harms, Notizbl. Bot. Gart. Berlin-Dahlem 9: 295. 1925.

At the time I was working on the first monograph of American *Erythrina* (Krukoff, 1939) two collections of this species were available: the holotype (*Rimbach 307*), which was subsequently lost in Berlin and *Rimbach 836* (F, MAD). Both are from Ecuador, from the provinces Chimborazo and Los Ríos (2,500–2,600 m altitude), and both were in flower, in July and September respectively. In Suppl. III (Krukoff 1969: 123) are cited two more specimens: *Acosta Solis 5847* (F), and *6847* (F), from the province of Bolívar (at 1,300 and 2,600–3,000 m alt.). No other specimens have been collected to date.

Pods and seeds of this species are unknown and we do not know whether the inflorescences are cauliflorous.

18. *Erythrina schimpffii* Diels, Biblioth. Bot. 116: 96. 1937.

Ecuador: Azuay: about 3 km from Guayas, ± 1050 m, *J. D. Boeke 2186*.

This species is known from 19 collections, all from Ecuador (provinces of Guayas, Pichincha, Tungurahua, Imbabura, Los Ríos, Cotopaxi, Bolívar, Chimborazo, Cañar, Pastaza, El Oro, Azuay) at elevations of 270 to 1,600 m. Inflorescences are borne on old wood (Camp, Plowman); flowers (standards) are described by several collections as "bright orange" or "crimson orange."

In routine identifications *E. schimpfii* is immediately distinguished from the related *E. polychaeta* as its petioles, petiolules and leaflets are spineless or very sparsely and irregularly aculeate, whereas those of *E. polychaeta* are regularly setose-aculeate (including both faces of the leaflets).

Plowman 5457 through a typographical error was cited as "*3457*" (Suppl. IX, Krukoff, 1977a).

19. *Erythrina montana* Rose & Standley, Contr. U.S. Natl. Herb. 20: 179. 1919.

Mexico: Nyarit: *W. D. Stevens 1474* (MEXU); Durango: steep rock, slopes, *Bennett 808* (MO).

20. *Erythrina leptorhiza* Alph. DeCandolle, Prodr. 2: 413. 1825.

Mexico: Michoacán: cima del Cerro de las Varas, ± 2400 m, *Grupo Etnobiología 192* (5/27-1978).

21. *Erythrina horrida* Alph. DeCandolle, Prodr. 2: 413. 1825.

Mexico: Oaxaca: *Mario Sousa 6052* (MO, MEXU) al pie del Cerro San Filipe, ± 1850 m).

21a. *Erythrina* (Sect. *Leptorrhizae*) *sousae* Krukoff & Barneby, sp. nov.—Fig. 1.

Ab aliis sectionis speciebus calyce longidentato (dente dorsali lineari-lanceolato 9.5–12 mm longo) eximie diversa.

A small shrub, leafy at anthesis; petioles 19–30 cm long, glabrous, occasionally aculeate; petiolules 6–11 mm long soon glabrous; leaf blades chartaceous, glabrous throughout (except veins often puberulent), not aculeate on the costa and veins above and beneath; terminal leaflets broadly ovate-deltoid or suborbicular, 11.5–15.5 cm long, 11–13.5 cm broad, acute at the apex; secondaries ± 6 per side, the veinlets prominent on both surfaces; rachis 21–27 cm long, softly puberulent, soon glabrate, usually aculeate; pedicels ± 8 mm long, puberulent; calyx salmon (ex Sousa) thin-chartaceous, campanulate, ±14–15.5 mm long on the carinal side, ± 19 mm long on the vexillar side, ± 3 mm broad at the base, ampliate to ± 6 mm at the apex, the margin 5-dentate, the dorsal tooth 9.5–12 mm long, the rest shorter; standard erect, red, 55–60 × 9–12 mm; wings linear-elliptic, 9–10 × 1.5–2 mm; keel petals united by the exterior margins, the blade when laid out broadly oblong-obovate, shallowly emarginate, 17 × 8 mm; ovary and gynophore softly pubescent.

Mexico: Oaxaca: district Pochutla, 14 km SSW of San Miguel Suchixtepec, ± 2100 m, *Mario Sousa S. 7563* (June 23, 1977), (NY—holotype, MEXU) *5612* (April 24, 1976) (MEXU) 18 km SW of Suchixtepec, carr. Pochutla—Oaxaca, ± 1700 mm.

The collector describes the plants as *shrubs*, ± 1 m high, rather rare, growing in pine forest.

This species is related to *E. horrida* which is however a perennial herb, not a shrub, with the pods and ovary shortly aculeate after anthesis. It is immediately distinguished from *E. horrida* and other members of Sect. *Leptorhizae*, as well as other species of *Erythrina* native to Mexico, by the long teeth on the calyx such as also occur in the unrelated *E. peruviana* of Sect. *Corallodendra*. Its large cuplike stipules recur only in the unrelated *E. poeppigiana* of Sect. *Micropteryx* and in *E. subumbrans* of Sect. *Hypaphorus*. Its keel petals distinguish this species from all known species of *Erythrina*. They are ± 3 times shorter than the standard, broadly oblong-obovate, and shallowly emarginate.

24. *Erythrina flabelliformis* Kearney, Trans. New York Acad. Sci. 14: 32. 1894.

Mexico: Michoacán: *Grupo Etnobiología 111* (Jan. 28, 1978).

25. *Erythrina coralloides* Alph. DeCandolle, Prodr. 2: 413. 1825.

Mexico: Distr. Fed.: Ciudad Univers., ± 2250 m (cult.) *R. Hernández M. 1735*

Erythrina sousae Krukoff

(M. Sousa 7563; x 2)

FIGURE 1. Dissected flower of *Erythrina sousae* Krukoff.

(11/17-1972—flrs.) (MEXU), *1856* (2/2-1973—flrs.) (MEXU), *1919* (4/27-1973—frts.) (MEXU).

26. *Erythrina* aff. *coralloides* Alph. DeCandolle.

Mexico: Querétaro, ± 1900 m, *Elizabeth Arguelles* 388 (flrs.) (MEXU); Michoacán: mun. Tzinzunzan, Ichupio, *Grupo Etnobiología 121* (1/28-1978).

27. *Erythrina pudica* Krukoff & Barneby, Phytologia 27: 114. 1973.

Additional collections of this species, which is known only from three collections in the state of Chiapas, Mexico, are desirable. Pods and seeds are not known.

28a. *Erythrina lanata* Rose subsp. *lanata*.

Erythrina lanata Rose, U.S.D.A. N. Amer. Fauna 14: 81. 1899.

Mexico: Michoacán: *Mario Sousa 8014* (El Cangrejo, a 16 km al NE de la Huacana, ± 1050 m), *H. Hernández 5*.

28c. *Erythrina lanata* subsp. *calvescens* Krukoff, subsp. nov.

A subsp. *occidentali*, remote allopatrica, praesertim calyce glabrato, a subsp. *lanata* insuper vexillo parce hirtello (nec dense albo-lanato) absimilis.

Mexico: Oaxaca: *Mario Sousa 5506* (a 6 km al SE de Cacahuatepec), *7056* (a 2 km al SE de Pinotepa Nacional) (NY—holotype), *7452* (camino a playa Chipehua, a 37 km al SW de Salina Cruz, distr. Tehuantepec), *7493* (Los Tunillos, a 2 km al ENE de la Reforma, distr. de Yautepec), *7541* (a 13 km al E de Tutolapan, distr. de Tlacoluia), *7586* (a 14 km al E de Pochutla, distr. de Pochutla), *7642* (a 4 km al NNE de San Gabriel Mixtepec, distr. de Juquila).

The collections cited above are from shrubs or small trees 2–5(–6) m high found at low elevations, from sea level to 700 (1,150) m.

Below is a key to the three subspecies of *E. lanata* and two related species.

1. Standard glabrous, even in very young flowers.
   2. Calyx glabrous ..... *E. goldmanii*
   2a. Calyx lanate ..... *E. pudica*
1a. Standard densely lanate dorsally or sparsely hirtellous with fine hair, especially on young flowers.
   3. Standard densely lanate ..... *E. lanata* subsp. *lanata*
3a. Standard thinly hirtellous.
   4. Calyx white tomentellous ..... *E. lanata* subsp. *occidentalis*
   4a. Calyx essentially glabrous ..... *E. lanata* subsp. *calvescens*

The new subspecies is immediately distinguished from the two other subspecies by the glabrous calyx. Leaflets and fruits (including a very conspicuous and broad black line near the hilum) are essentially like those in the two other subspecies.

Unfortunately, I have not seen the new subspecies in the field. As is the case with the two other subspecies of *E. lanata* and *E. pudica*, its standards are pink, but I do not yet know the color of its calyces, which are strikingly black in *E. goldmanii*. I also do not know whether the flowers and buds before anthesis are deflected from the floral rachis, the standard eventually forming an angle of about 45° from the vertical (as is the case with *E. pudica*).

In routine identification fruiting specimens of *E. lanata* subsp. *calvescens* were often confused in the past with *E. herbacea* subsp. *nigrorosea*. If mature seeds are available, they are immediately told apart as seeds of the former have a very distinct, broad, black line near the hilum, whereas in seeds of the latter, this line is not distinct.

In Suppl. VII (Krukoff & Barneby, 1973: 114–117) Barneby and I described the related *E. pudica* and reviewed at length the two subspecies of *E. lanata* (subsp. *lanata* and subsp. *occidentalis*). Besides differing in morphological characters of the flowers, they were found to have different distributional ranges. All presently examined collections from Oaxaca cannot be accommodated in the two previously known subspecies, as is evident from the key.

32. *Erythrina tuxtlana* Krukoff & Barneby, Phytologia 25: 11. 1972.

Additional collections of this species, known only from two collections from the type locality in mun. Tuxtepec, Oaxaca, Mexico, are desirable.

41. *Erythrina chiriquensis* Krukoff, Brittonia 3: 322. 1939.

Nicaragua: Matagalpa: Cordillera Dariense, Santa Maria de Ostuma, ± 1500 m, lower montane wet forest, *David Neill 2974* (MO). Costa Rica: Cartago: *Krukoff 1973-4* (Birrisito de Paraíso), *1973-5* (near Cartago), *1973-6* (Tres Ríos); *F. Almeda 4174* (CAS) (south slope of volcano Turrialba, ± 4400 ft); Alajuela: *Krukoff 1973-7* (near Zarcero), *1973-8, 1973-9, 1973-10.* Panama: Chiriquí: Cerro Punta, ± 6000 ft, *J. P. Folsom 3999* (MO).

Folsom's specimen is a voucher for seeds which are under chemical studies by Prof. Jackson.

Few, if any, erythrinas caused such difficulties as *E. chiriquensis*, and even now it is not completely understood. We still need good fruiting material from Nicaragua for which we have been waiting since 1973, also collectors' field observations of *fresh calyces.*

Erythrina chiriquensis was described by me in 1939 on the basis of a single collection in flower from Chiriquí, Panama (1,300–1,900 m). Now we have ample material (20 collections) from Panama. Dried specimens of it are remarkably uniform in all characters and have never caused any difficulties in identification.

Difficulties were, however, encountered when Rupert Barneby and I started to work on my collections from Costa Rica made in 1969. *Erythrina globocalyx* is found in Costa Rica which, as is the case with *E. guatemalensis* and *E. steyermarkii*, has ellipsoid, fleshy calyces, when fresh broadest in the middle and contracted at the mouth so as to clasp the petals and stamens. [See Barneby's drawings of calyces of fresh flowers of *E. globocalyx* and *E. steyermarkii* in Krukoff (1970: 20)]. This character, which is so striking in fresh flowers, cannot be observed in dried specimens, and we tried to tie this in with the thickness of the calyx. *Erythrina chiriquensis*, as represented from Chiriquí, has a definitely thickened calyx, not so thick, however, as *E. globocalyx* from the type locality (village of Los Nubes, San José, Costa Rica), but almost as thick as specimens from Zarcero, Alajuela, Costa Rica. As specimens from Costa Rica (from Los Nubes as well as from Zarcero) were collected by me, I was not prepared to accept Zarcero specimens under *E. globocalyx* as the plants are immediately told apart in fresh condition. They were cited under *E. chiriquensis* in Suppl. III, IV, and V (Krukoff, 1969, 1970, 1971).

In Feb. 1973 I made a special trip to Alajuela and Cartago in Costa Rica, collecting numerous specimens, and we came to the same conclusion. It is unfortunate that I never saw *E. chiriquensis* from the type locality in the field.

Several collections from the Cordillera Central de Nicaragua (1,200–1,500 m) in Dept. Matagalpa were placed under *E. chiriquensis* in Suppl. VIII (Krukoff 1976: 348), and again it is most unfortunate that I did not see any plants of this entity in the field.

Recently Rupert Barneby and I went over the entire problem again. Flowers (including keel petals and wings) and leaves in specimens from Chiriquí, and

Nicaragua are essentially alike, and we have to wait for collectors' observations of calyces of fresh flowers of plants from Chiriquí and Nicaragua and seeds from Nicaragua before reviewing this problem again.

Erythrina chiriquensis from Chiriquí has already been introduced to two gardens in Hawaii, and we must also introduce plants from Costa Rica and Nicaragua. The final word in this problem will probably come from genetic studies when we will be growing these plants in Hawaii side by side.

42. *Erythrina macrophylla* Alph. DeCandolle, Prodr. 2: 411. 1825.—FIG. 2.

El Salvador: Chalatenango: El Pital, *E. A. Montalvo 4821*. Guatemala: Jalapa: Pinula–Jalapa, *Oswaldo Téllez 602* (4/9-1978—flrs.); Chimaltenango, 8 km E of El Tejar, between El Tejar and Sumpange, or 12 km NW from Antigua, near the road from Guatemala to Chimaltenango, *Mario Sousa S. 4224* (Sept. 7, 1978—flrs.), *Krukoff 1978/21* Dec. 1978—flrs., frts.).

The above are new records for the departments of Chalatenango and Jalapa, in Guatemala and El Salvador, respectively. Specimens collected by Mario Sousa and later in the same locality by Krukoff need to be discussed. Sousa's collection is normal for the species in all respects except that the calyx is provided with five teeth 2–3 mm long (see Fig. 2). A special trip was made by me to the locality where this collection was obtained, and I ascertained that this unusual collection cannot be distinguished even as a form for, although the teeth on some of the specimens are long, there are many others which approach the more common form with smaller teeth. Incidentally, the fruits of these collections, as those of typical *E. macrophylla*, can be easily distinguished at a distance, as pods are only slightly constricted between the seeds and hang down in a very characteristic manner. Standards, keel petals, and wings, as well as leaves, are indistinguishable from the common form of the species. Furthermore, a rather thorough search in this locality resulted only in finding all gradations from Sousa's collection to a more common form. Krukoff's collection (in flrs. & in frts.), carefully chosen, represents an intermediate form with calyx teeth about 1 mm long.

45. *Erythrina steyermarkii* Krukoff & Barneby, Mem. New York Bot. Gard. 20: 175. 1970.

Nicaragua: Chontales: ± 400–500 m, *W. D. Stevens 6124*; Matagalpa: ± 370 m, *W. D. Stevens 6023*; Zelaya: *David Neill 3719* (along Caño Madriguera, ± 250 m), *4142* (Kuikuinita, ± 160 m), *W. D. Stevens* 6823 (MO) ± 600–800 m, *6893* (along Caño Majagua), *7375* (Cerro Waylawas, 100–268 m), *8819* (Siuna to Matagalpa), *Paul C. Vincelli 330A, 407* (along Caño el Toro).

This is the first record of this species from Matagalpa.

47. *Erythrina berenices* Krukoff & Barneby, Phytologia 27: 120. 1973.

Mexico: Veracruz: *A. Gómez-Pompa 1837* (Dec. 9, 1966) ± 1000 m), *Wilfrido Márquez M-851* (F) (Tlalnalhuayacan, ± 1400 m), *Vicente Vasquez Torres W279* (F) Zongolica, ± 1150 m).

This species was known previously from four collections, all from high elevations in the state of Veracruz and cited with the original description.

(M. Sousa 4224; x 2)

FIGURE 2. Dissected flower of *Erythrina macrophylla* Alph. De Candolle.

49. *Erythrina lanceolata* Standley, Contr. U.S. Natl. Herb. 17: 432. 1914.

Nicaragua: **Matagalpa: Sta. Maria de Ostuma**, ± 1300 m, *Antonio Molina 31623* (MO). Panama: Chiriquí, 2½ km from Questa Piedra along Río Monte road, *J. P. Folsom 3986* (MO).

This is the first record of the species from the province of Chiriquí.

50. *Erythrina costaricensis* M. Micheli, Bull. Herb. Boissier 2: 445. 1894.

Panama: **Coclé:** *J. P. Folsom 5637* (MO), *6435* (MO), *Barry Hammel 3848* (MO); **Colón:** *G. A. Sullivan 139* (MO).

This is the first record of the species from the province of Coclé.

52. *Erythrina americana* Miller, Gard. Dict., ed. 8, no. 5. 1768.

Mexico: San Luis Potosí: Tamanzunchale, *Mary Taylor Edwards 682* (MO).

This is the first record of the species from San Luis Potosí.

53. *Erythrina berteroana* Urban, Symb. Ant. 5: 370. 1908.

Nicaragua: *Seemann 26* (1867) (BM); Managua: *W. D. Stevens 4543* (800–860 m), *5136, 5817* (800–900 m) (flrs. & frts.—Jan. 6), *6191* (flrs. & frts.—Jan. 28); Masaya: *David Neill 2811* (MO), *3120* (MO), *W. D. Stevens 5258*; Granada: foot of Volcán Momacho, *David Neill 2726*; Estelí: *W. D. Stevens 5772, 9088*; Matagalpa: *David Neill 848* (Matagalpa–Jinotega, 1100–1300 m), *W. D. Stevens 6007* (± 1100 m), *6024* (± 335 m); Boaco: *J. D. Atwood 3834* (F), *W. D. Stevens 5830* (± 275 m); Chontales: *W. D. Stevens 3664, 4177* (350–400 m). Panama: Chiriquí: *J. P. Folsom 3936* (MO), *3957* (MO); Canal Zone: *J. P. Folsom 3661, 3662, 3663, 3664.*

This is the first record of the species from Masaya. Six Folsom specimens are vouchers for seeds under chemical studies by Prof. Jackson.

54. *Erythrina rubrinervia* H. B. K., Nov. Gen. & Sp. 6: 434. 1824.

Panama: Veraguas: valley of Río Dos Bocas, 450–550 m, *Croat 27763* (MO). Colombia: Antioquia: *John D. Sheperd 665* (MO).

These are the first records of these species from the department of Antioquia and from the province of Veraguas.

55. *Erythrina mexicana* Krukoff, Brittonia 3: 309. 1939.

Mexico: Zacatecas: *Kalil S. Boghdan 39356* (A); Hidalgo: mun. Ilanchinol, *Emma Estrada Martínez 192.*

This is the first record of the species from Zacatecas and Hidalgo.

56a. *Erythrina santamartensis* Krukoff & Barneby, Phytologia 33: 350. 1976.

Colombia: Sierra Nevada de Santa Marta, ± 200 m, *E. W. Davis 561.*

This is the third collection of this species. The collector states on the label: "seeds red and black." This statement is intriguing but search in the Harvard herbaria, including the fruit collections, failed to locate pods or seeds of this collection.

57. *Erythrina castillejiflora* Krukoff & Barneby, Mem. New York Bot. Gard. 20: 165. 1970.

The tree from which the type material was collected was cut down, and repeated attempts to find another one failed. Incidentally, this is one of the three species of which young leaves and flowers are consumed in soups and salads; the others are *E. berteroana* and *E. americana*. At times I have doubts that it is a distinct species. Perhaps it is a hybrid of *E. berteroana*, but there is not a single other species of *Erythrina* in the type locality which could be considered as another parent. As it was collected in a disturbed forest area, perhaps it was introduced from the completely uncollected, vast, lowland virgin forest on the Río Ixcán, a tributory of the Río Usumacinta in the departments of Huehuetenango and Quiché in Guatemala.

58. *Erythrina gibbosa* Cufodontis, Arch. Bot. Sist. 10: 34. 1934.

Nicaragua: Zelaya: *W. D. Stevens 4797* (200–300 m), *5066* (Caño Costa Riquita).

This is the first record of this species from Nicaragua.

59. *Erythrina amazonica* Krukoff, Brittonia 3: 270. 1939.

Peru: Junín: Satipo, ± 350 m, semi-arid cactus-acacia forest, *M. T. Madison 10453-70* (F). Ecuador: Napo: *E. W. Davis 424* (AAU) (± 750 m, used commonly for fence posts).

This is the first record of the species from Junín. It is a poorly known species, which perhaps consists of distinct subspecies or forms. I have seen collections with all red and others with red and black seeds. The study of this species is difficult as it is confined to special habitats, in widely separated regions. The closely related *E. similis* is known from the type collection (region of Lake Ypacaray, Paraguay) and two poor and old collections, one from Bolivia and another from Mato Grosso, Brazil. Repeated attempts failed to produce new collection of this. Once the distribution of *E. amazonica* is well known, *E. similis* might become a subspecies of it.

63. *Erythrina pallida* Britton & Rose, Bull. Torrey Bot. Club 48: 332. 1922.

Trinidad: Simla: *Peter Feisinger s.n.* (Febr. 1978).

This is a voucher for seeds which are under chemical studies by Prof. Jackson.

64a. *Erythrina corallodendrum* L. var. *corallodendrum*

Erythrina corallodendrum L., Sp. Pl. 706. 1753.

It will probably never be possible to completely know the original ranges of distribution of the three varieties of *E. corallodendrum* as they are almost extinct in the wild but extensively cultivated and/or escaped from cultivation.

67. *Erythrina leptopoda* Urban & Ekman, Ark. Bot. 20A(5): 14. 1926.

Dominican Republic: Manigua: cerca de Ciénaga de Monabáo, Jarabacoa, ± 900 m, *A. Liogier 24366.*

This is the first record of this species from the Dominican Republic. It was known previously from eight collections from Haiti, all collected by H. Ekman and all cited in Krukoff (1939: 305–307).

68. *Erythrina elenae* Howard & Briggs, J. Arnold Arbor. 34: 183. 1953.

Erythrina linearifoliata Areces, Ciencias, Ser. 10, Bot. (Univ. Habana) 3: 11. 1975.

In the original description of *E. linearifoliata* it is stated that an isotype was sent to JE. On April 20, 1977, I received a communication from this herbarium to the effect that, up to that date, this specimen had not been received at Herbarium Haussknecht, Jena.

70. *Erythrina oliviae* Krukoff, Phytologia 19: 128. 1969.

Mexico: Puebla: El Papayo, *Mario Sousa 7197* (flrs.—Apr. 12, 1977, leafless), *H. Hernández s.n.* (Apr. 15, 1978) (MEXU), *1* (Chinantla) (MEXU); Michoacán: *M. T. Germán 409* (km 227 de la carretera Arteaga—Infiernillo) (May 21, 1977—flrs.) (MEXU), *H. Hernández 2* (May 23, 1978) (sobre la carretera que va del entroque de Ruta Nueva Italia-Arteaga a la presa del Infiernillo).

This is the first collection of this species outside of the type locality in the Oaxaca Desert, and it is a new record from the state of Michoacán. Mario Sousa reports that they made a special trip to the type locality of *Erythrina oliviae* to collect a specimen of it, and then they found it in the state of Michoacán.

72. *Erythrina lysistemon* Hutchinson, Bull. Misc. Inform. 1933: 422. 1933.

Rhodesia: Salisbury, cult., *T. Müller 2703* and *2704*.

These are vouchers for seeds which are under chemical studies by Prof. Jackson.

76. *Erythrina greenwayi* Verdcourt, Kew Bull. 25: 175. 1971.

Tanganyika: Iringa District, *P. J. Greenway & Kanuri 14814* (BM).

78. *Erythrina vogelii* Hooker f., Niger Flora 307. 1849.

Upper Volta: *C. Geerling 1086* (MO) (Sindou, savanna), *1215* (MO) (Bobo–Dioulasso, in creek ravine), *1631* (MO) (3 km E of Bouna).

These are the first three collections of this species seen by me from Upper Volta.

79. *Erythrina senegalensis* Alph. DeCandolle, Prodr. 2: 413. 1825.

Sierra Leone: *coll. undesign. s.n.* (Herb. Lamb.) (BM) (holotype of *E. guineensis* G. Don).

82. *Erythrina pygmaea* Torre, Bol. Soc. Brot., sér. 2, 39: 213. 1965.

I hope to see additional material of this species known from a single poor specimen in fruit. It was collected in Angola.

83. *Erythrina mendesii* Torre, Bol. Soc. Brot., sér. 2, 39: 212. 1965.

Botswana: *P. A. Smith 1872* (K) (26/12-1976—flrs.).

This is the first record of this species from Botswana.

88. *Erythrina addisoniae* Hutchinson & Dalziel, Bull. Misc. Inform. 1929: 17. 1929.

Ghana: Kumasi: *A. A. Enti FE-1821*.

This is a voucher for seeds which are under chemical studies by Prof. Jackson.

92. *Erythrina haerdii* Verdcourt, Kew Bull. 24: 285. 1970.

Additional material of this species, native to Tanzania, is needed. Pods and seeds are not yet known.

93. *Erythrina sigmoides* Hua, Bull. Mus. Hist. Nat. (Paris) 3: 327. 1897.

Senegal: Niokolo-Koba N. P., *C. E. G. Tutin 43* (K).

This is the first collection of the species seen by me from Senegal.

95. *Erythrina abyssinica* Lamarck, Encycl. Bot. 2: 392. 1788; ex Alph. DeCandolle, Prodr. 2: 413. 1825; Gillett, Kew Bull. 15: 426. 1962.

Kenya: Kilima Kiu, Machakos District, *Prescott Decie s.n.* (1914) (syntype of *E. platyphylla* Baker f.). Angola: highlands of Golongo Alto, *Welwitsch 2229* (BM) and *2230* (BM) (syntypes of *E. suberifera* Welwitsch); Huilla: 3800–5500 ft, *Welwitsch 2231* (BM) (holotype of *E. huillensis* Welwitsch). Rhodesia: Salisbury: *T. Müller 2705*.

Müller's specimen is a voucher for seeds which are under chemical studies by Prof. Jackson.

96. *Erythrina variegata* L., Herb. Amboin. 10. 1754; Amoen. Acad. 4: 122. 1759, based on *Gelala alba* Rumphius, Herb. Amboin. 2: 234, *tab*. 77. 1750.

Australia: Queensland: *M. Lawrie s.n.* (Sept. 1971) (Dawan Island), *Everist 9696* (Goold Island), *D. R. Stoddart 4247* (Green Island), *7266* (South Island), *C. T. White 10123* (Hayman Island), *M. Lawrie 100, 105* (Murpay Island), *L. S. Smith 4857* (Bingil Bay), *L. J. Webb 3021* (Mission Bay), *J. G. Tracey 3353, V. K. Moriarty 1574* (Clump Point, edge of rain forest on beach), *S. A. Renvoize 1335* (US).

In Suppl. X (Krukoff, 1977b: 409) I stated: "The above eight specimens are irrefutable evidence that this species is native to Northern Australia and not introduced for cultivation." The 12 specimens cited above not only confirm this statement but also indicate clearly that this species in northern Australia is common on the Islands and on the shore of the ocean in Northern Territory and Queensland.

97. *Erythrina tahitensis* Nadeau, Enum. Pl. Tahiti 80. 1873.

Hawaii: *Glen Spence s.n.* (July 17, 1978).

I have been waiting for many years to grow plants of this species from Hawaii and Tahiti side by side. We will have this opportunity before long. Recently this species has been found in Tahiti and plants are being grown in Hawaii in the Pacific Tropical Botanic Garden as well as in the Waimea Arboretum.

As predicted (Krukoff, 1972: 137), this species is not extinct in Tahiti and is found on very steep slopes. It was found by S. Perlman with help of guide Henri Jay on the western side of Tahiti, at Mapura (±2,000 ft). Mr. Jay stated that he knows four other trees from the Popenoe valley, on the eastern side of Tahiti.

98. *Erythrina euodiphylla* Hasskarl, Hort. Bogor. 178. 1858.

East Java: *C. Backer s.n.* (Oct. 1907—flrs.) (Tandjonj Prook, cult., "flrs. green") (BO) this is the note which gave the wrong information that the flowers in this species are green, which error was repeated by several subsequent workers), *Herb. Bogor 2-0-10* (seeds) (cult.) (BO) (some seeds may not belong here, they resemble those of *E. variegata*), *2-0-16* (flrs.) (cult.) (BO), *Herb. Hort. Bogor 4701* (flrs., frts.) (BO), (these are the pods and seeds from which Rupert Barneby made a drawing published in Lloydia 37: 434. 1974), *Herb. Bogor 837*

(11/8-1922—flrs.) (Soerabaja) (BO), *879* (29/8-1922) (Soerabaja) (BO), *D. T. H. 3870* (Soerabaja) (BO), *R. van der Veen s.n.* (Febr. 1979) (seeds only collected at Baluran Nature Reserve) (MO, NY) (seeds closely resemble those of *E. variegata*; they are now planted in two Botanical Gardens in Hawaii and in 2–3 years, at which time the plants will be in flower, their identity will be known.

After a search of all *major* herbaria in the Orient, Europe, and the United States, I ascertained that this species is represented only by two collections in Leiden and by several specimens in Bogor. This does not mean that it is rare or an "endangered species." It is merely found in a seldomly collected region ("savanna of man-size grasses and scattered trees"). Its best field description is found on *M. Jacobs 4886* (24/5-1951) collected at Besuki, S foot of Mt. Baluran Game Preserve, 1–6 km N of Wonokedje, 114° 20′ E, 7° 50′ S. The collector states that it is a "tree 8–10 m with rough bark, leafless, flrs. odorless, *standard fulvous-ochreous*, other petals glossy green-brown, filaments red, paler toward base, anthers dark brownish or white floccose, style red, stigma green. Common."

This information was confirmed by van der Veen in July 1975 when he obtained specimens in flower and made slides.

99. *Erythrina vespertilio* Bentham in Mitch., J. Trop. Austr. 218. 1848.

Erythrina biloba F. v. Müell. in Hooker's J. Bot. Kew Gard. Misc. 9: 21. 1857.

Dr. J. R. Maconochie supplied us with useful information on the two type collections:

The type collection of *Erythrina vespertilio* Benth. Label Data:

1846 No. 189, June 29/46
Thorny shrub. sub-Trop. New Holland
Lieut.-Co. Sir T. L. Mitchell

From Mitchell's Journal, they spent that day (29) travelling along the left bank of a newly found river. On the 30th June Mitchell recorded collecting a new *Erythrina*—a thorny shrub and from his map its approximate locality is 25° S and 147° 30′ E.—The Warrego District of Queensland.

The type collection of *Erythrina biloba* F. v. Müeller

F. Müell's label at K: "This was nowhere seen but on the foot of a little Granite Range at the head of Hooker's Creek and Sturt's Creek. It bore neither flowers nor fruits but I found two or three grains of seeds and a few half damaged valves. We intended to revisit the spot on our return but took a straight course across the country (viv. map) and thus I could not procure more specimens."

This location was reached about 15 January, 1856 and the head of these two creeks is approximately 18° lat., 130°E long.—in Northern Territory.

Dr. P. R. Wycherley kindly supplied me with very interesting information on the occurrence of this species and on the flowering and fruiting seasons in Western Australia:

The nearest *Erythrina vespertilio* is nearly 900 miles from Perth and it occurs sporadically in small groups of trees near river beds along a further 1200 miles to the north western extremity of Western Australia, about 2000 miles from Perth by road, most of the latter part being on unsealed roads. Four-wheel drive vehicles are essential for any field work. One can sometimes save time by flying and hiring local transport, but usually at greater cost. Recent survey work in the north west has used helicopters.

Although the flowering and fruiting seasons can be predicted in general terms, in practice

much depends on the vagaries of each year. The northwest is a mainly summer rainfall area by contrast with winter rains in the south west. Too soon and the seed is unripe. Even a day or two late and the dehiscent pods have thrown out their seeds.

Dr. L. Pedley of the Queensland Herbarium recently sent me two photographs of *E. vespertilio* (typical form) with white flowers (standards). This is the first record of such flowers in this species. I already reported earlier in this paper of the occurrence of white flowers in *E. verna* and *E. herbacea* subsp. *herbacea*. Such flowers are seen occasionally in several other species, and it is desirable to incorporate some of the white-flowered plants in our genetic studies in Hawaii. I am now trying to obtain seeds of *E. vespertilio* with white flowers.

101. *Erythrina merrilliana* Krukoff, J. Arnold Arbor. 20: 227. 1939.

New Guinea: Madang District: rain forest, ± 40 m, *P. Katik 46673*.

This is the first record of the species from Madang District. It was known previously from Central, Morobe, and Milne Bay District.

102. *Erythrina velutina* Willdenow, Ges. Naturf. Freunde Berlin Neue Schriften 3: 426. 1801.

Brazil: Rio Grande do Norte: *A. Castellanos 22820* (R); Sergipe: Japaratuba, *Herb. Jard. Bot. Rio 175067*.

These are the first records of the species from Rio Grande do Norte and Sergipe.

102a. *Erythrina velutina* Willdenow f. *aurantiaca* (Ridley) Krukoff, Brittonia 3: 329. 1939.

Paraiba: estradu entre São João da Cariri and Serra Branca; *J. Mattos 9768* (SP), *s.n.* (21/2-1962) (SP).

It is very satisfactory that *E. aurantiaca* Ridley was reduced to a form as we now have more evidence that it is neither a species or subspecies. Dr. Dardano A. Lima told me that during his visit to the Island of Fernando Noronha (the type locality of *E. aurantiaca* Ridley) he observed that the majority of the trees there have red seeds and only a few have red and black seeds. Trees with seeds red and black were found recently in Ceará and Paraíba.

In numerous collections of *E. pallida* seeds are invariably scarlet with ¼ or ⅕ of the seeds black, so this character is consistent. The same might be said concerning *E. perrieri*, although there are not too many collections known of this species. On the other hand, there are races of *E. amazonica* which have seeds scarlet and black in about ⅕ of the seeds. Seeds of this species, as it is presently understood, are usually red.

We now have plants of *E. velutina* f. *aurantiaca* grown from red and black seeds (collected in Brazil) in Hawaii, side by side with plants grown from red seeds.

Matto's specimens from Paraíba have seeds red and black in about ⅕ of the seeds.

103. *Erythrina grisebachii* Urban, Symb. Ant. 9: 453. 1928.

E. grisebachii was retained in the first monograph (Krukoff, 1939) as a good species largely because of the size of its flower. I stated: "I retain Urban's species for the time being, but field studies may prove that it is better regarded as a variety or an ecological form of *E. velutina*." The following facts should be taken into consideration in making a decision on this name:

1. Specimens of *E. grisebachii* are from trees grown on *rich* soils of Cuba, mostly from street trees, etc. If they are compared with specimens taken from trees grown on poor soils in desertlike countries (to which *E. velutina* is largely confined), these flowers are at least two times larger.

2. Typical *E. velutina* occurs in Cuba.

3. We now have specimens, such as *Epling 496* from Ecuador, with very large flowers.

4. *Box 1410* from Antigua has flowers indistinguishable from *E. grisebachii* which is supposed to be endemic of Cuba. The collector notes on the label, "There are probably less than half a dozen of these trees in the Island growing apparently wild in the higher parts of the central region."

5. *Luiz Emygdio 2133* from Rio de Janeiro also has large flowers.

The problem with *E. grisebachii* could be solved satisfactorily only by horticultural testing. The difficulty is that up to the present we were unable to obtain seeds of *E. grisebachii* from Cuba for growing in Hawaii.

It is interesting that a more or less similar situation exists with the extremely variable and widespread *E. variegata*. Some specimens from New Caledonia deposited at P have the smallest flowers for this species, at least three times smaller than those of specimens of some races in India or elsewhere. Of course, I do not know in what ecological conditions this species is growing in New Caledonia.

105. *Erythrina burana* R. Chiovenda, Atti Reale Accad. Italia, Mem. Cl. Sci. Fis. 11: 27. 1940.

Ethiopia: Addis Ababa: (cult.), *Mesfin Tadesse s.n.* (July 18, 1978).

This is a voucher for seeds which are under chemical studies by Prof. Jackson.

107. *Erythrina schliebeni* Harms ex Mildbraed, Notizbl. Bot. Gart. Berlin-Dahlem 12: 512. 1935.

Additional collections, especially of fruits and seeds, which not yet are known, are needed to compare with those of *E. perrieri*. Flowers and especially calyces of these two species are suspiciously similar.

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CHEMICAL CONSTITUENTS OF THE NECTARS OF TWO *ERYTHRINA* SPECIES AND THEIR HYBRID[1]

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Abstract

In an analysis of sugars, amino acids, and other substances (lipids, antioxidant organic acids, phenolics, alkaloids, proteins) of nectar, the hybrid *Erythrina* × *bidwillii* showed a quantitative intermediacy and qualitative additiveness in amino acids compared to its parents, *E. herbacea* and *E. crista-galli*, and intermediacy in sugars and the other compounds.

In two recently published papers (Baker & Baker, 1976a, 1977) we have shown that the floral nectar amino acid complements of closely related species in several genera of flowering plants are intraspecifically surprisingly constant, although usually interspecifically different. In the F_1 hybrids between the species, the complements are additive on a qualitative basis (although not necessarily so quantitatively). Indirect evidence has been accumulated that shows genetic segregation in subsequent hybrid generations, and the inheritance of amino acid production is under experimental study in *Geranium* and *Silene*.

In two other papers (Baker, 1978; Baker & Baker, 1980) we have shown that the relative proportions of the three common sugars in nectars (sucrose, glucose and fructose) from a wide range of species are, to some extent, determined by the taxonomic affinities of the species concerned, but also show adaptation to the type of pollinator whose services are used by that species. However, we have not been able to find evidence in the literature as to the inheritance of nectar sugar characteristics. This lacuna, together with the fact that none of our studies of amino acid inheritance has involved trees, suggested that attention should be given to the chemical constituents from *Erythrina*. The present paper is a preliminary study which it is hoped may become more nearly comprehensive in the future.

For *Erythrina* we have provided evidence that the relative proportions of sucrose and hexose sugars in the nectars of some hummingbird-pollinated species (viz., high sucrose:hexose ratios) are different from those of some other species where pollination is by passerine birds (viz., low sucrose:hexose ratios) (Baker, 1978; Baker & Baker, 1980; see also Feinsinger & Bolten, this symposium). The demonstration of this pollinator-related difference was foreshadowed in the data we provided for Cruden & Toledo (1977) in their comparison of *E. coralloides* A. DC. (hummingbird pollinated) with *E. breviflora* A. DC. (pollinated by orioles and tanagers). We also showed (Baker, 1978) that the complement of amino acids in *E. breviflora* was larger, and included all of the "essential" amino acids, as well as being more concentrated.

On the basis of the sugar proportions in its nectar (Baker & Baker, 1980) and

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[1] We are grateful to Dr. Jack B. Fisher for collecting nectar from *Erythrina herbacea* subsp. *herbacea* in Florida. This work was assisted by funds generated by N.S.F. Grant no. DEB 76-19919, for which we are thankful.

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an absence of reliable observations of hummingbird pollination of trees in their native South America (see Toledo, 1974), we suggested (Baker & Baker, 1980) that *Erythrina crista-galli* L. may also turn out to be pollinated by passerine birds. Consequently, it is of interest to compare nectar analyses of this species with those of a species that is a member of the same genus and known to be pollinated by hummingbirds (Toledo, 1974). This is *Erythrina herbacea* L. Although placed in separate subgenera by Krukoff & Barneby (1974), these species can be hybridized. They have the same chromosome number, $2n = 42$ (Atchison, 1947).

With woody plants such as the erythrinas, it has not been feasible to make artificial hybrids for the special purpose of chemical analyses of their nectars. Consequently, advantage was taken of the existence of a horticultural hybrid between these species, *Erythrina* × *bidwillii* Lindley. Although this hybrid may have been made more than once since its original production by J. C. Bidwill over a century ago (Krukoff & Barneby, 1974), there is no evidence that generations after the F_1 have been raised, propagation being by rooting of cuttings. Consequently, we believe that the tree of *E.* × *bidwillii* growing in the University of California Botanical Garden in Berkeley, is very probably an F_1 hybrid. The accession cards at the Garden indicate that the tree (#50.1853) was received from the horticultural firm of Evans and Reeves, Los Angeles, in 1950. A tree of *E. crista-galli* also grows in the U.C.B. Garden (#34.489). It is derived from seeds, collected in South America, by Dr. T. H. Goodspeed. The identities of these trees were checked with descriptions in the latest monograph of the genus (Krukoff & Barneby, 1974) and compared with herbarium specimens. Our own herbarium specimens are in UC.

Graham & Tombs (1974) report that *Erythrina* × *bidwillii* has approximately 76% good pollen while the figure for *E. crista-galli* is about 88%. Our plants gave similar estimates.

Nectars from these trees were collected in the Botanical Garden in 1977 and 1978 and nectar of *Erythrina herbacea* subsp. *herbacea* was collected from a wild plant growing in a "hammock" within the Fairchild Tropical Garden, Coral Gables, Florida, in April 1978 by Dr. J. B. Fisher. There can be no doubt as to its identity as, in addition to its subshrubby habit, this is the only species growing wild in Florida. These nectar samples were immediately spotted onto chromatography paper, dried and used for analyses.

Methods of Analysis

SUGARS

Analyses of the sugars in these nectars were carried out by the method described by Baker & Baker (1980). In summary, it is a single direction, descending paper chromatographic analysis, using n-propanol:ethyl acetate:water mixture as a solvent, with staining by oxalic acid in ethanol mixed with p-aminobenzoic acid in chloroform and acetic acid. After drying and heating, the chromatograms are examined under U.V. illumination, in which all sugars fluoresce. The amounts of each sugar are estimated by eluting the individual sugar spots with methanol and measuring their fluorescence in a filter fluorometer. Calibration curves for

TABLE 1. Proportions of sugars in nectars of two *Erythrina* species and their hybrid.

Sugar	*E. crista-galli*[a] (1977)	(1978)	(1978)	(1978)	*E.* × *bidwillii*[b] (1977)	(1978)	*E. herbacea*[c] (1978)
Melezitose	N.D.[d]	0.009	0.007	0.008	N.D.[d]	0.014	0.017
Maltose	0.010	0.017	0.017	0.014	N.D.[d]	N.D.[d]	N.D.[d]
Sucrose	0.031	0.033	0.034	0.028	0.172	0.182	0.394
Glucose	0.396	0.464	0.406	0.403	0.450	0.421	0.318
Fructose	0.553	0.476	0.533	0.546	0.378	0.384	0.272
Ratio sucrose:hexoses	0.032	0.035	0.037	0.030	0.208	0.226	0.668

[a] Four determinations
[b] Two determinations
[c] One determination
[d] N.D. = not detected

each sugar correlating fluorescence with amounts of the sugar present are then used to estimate the proportions of the sugars present in the nectar.

AMINO ACIDS

Amino acid complements were identified and the relative proportions of each amino acid present in each nectar were estimated by the dansylation–U.V. fluorescence method described in detail by Baker & Baker (1976a, 1976b).

OTHER SUBSTANCES

Qualitative tests for lipids (OsO_4 test), antioxidant organic acids (2,6-dichlorophenol-indophenol test), phenolics (p-nitraniline test) and alkaloids (iodoplatinate and Dragendorff tests) were also made. Proteins were tested for by the brom-phenol blue method. For details of these test methods see Baker & Baker (1975), except for the test for phenolics which follows the method of Gray, Thorpe and White (Smith, 1969: 434).

RESULTS

SUGARS

The sugar analyses (Table 1) show a consistent pattern of hexose dominance in *Erythrina crista-galli*, sucrose richness (but not dominance) in *E. herbacea*, and an intermediate picture in *E.* × *bidwillii*. Also intermediate is the showing of the trisaccharide melezitose (which is slightly more concentrated in *E. herbacea*). The disaccharide maltose was hard to detect in *E. crista-galli* and could not be detected in *E.* × *bidwillii* and *E. herbacea*.

AMINO ACIDS

The amino acid analyses (Table 2) show that both species produce nectar with a large number of amino acids (21 for *Erythrina crista-galli*; 20 for *E. herbacea*). However, there are slight differences in the complements: *E. herbacea* lacks methionine in our analysis and the two species have different "unknown" amino acids (presumably of a "nonprotein" nature). *Erythrina* × *bid-*

TABLE 2. Amino acid complements of two *Erythrina* species and their hybrid. The proportions of each acid in the total for each taxon are shown.

Amino acid	*E. crista-galli*	*E. × bidwillii*	*E. herbacea*
Alanine	0.101	0.089	0.039
Arginine	0.069	0.028	0.004
Asparagine	0.065	0.111	0.174
Aspartic	0.006	0.024	0.036
Cysteine, etc.	0.003	0.019	0.018
Glutamic	0.006	0.047	0.038
Glutamine	0.202	0.177	0.231
Glycine	0.016	0.029	0.054
Histidine	0.012	0.008	0.025
Isoleucine	0.065	0.044	0.043
Leucine	0.017	0.017	0.036
Lysine	0.025	0.028	0.032
Methionine	0.014	0.018	N.D.[a]
Phenylalanine	0.023	0.039	0.027
Proline	0.075	0.075	0.076
Serine	0.074	0.058	0.028
Threonine	0.071	0.041	0.024
Tryptophan	0.010	0.022	0.029
Tyrosine	0.019	0.037	0.009
Valine	0.098	0.067	0.058
Unknown #1	0.013	0.006	N.D.[a]
Unknown #2	N.D.[a]	0.018	0.022

[a] N.D. = not detected

willii shows every one of the amino acids recorded for each plant (22 total) in the usual qualitative "additive" pattern for F_1 hybrids. For most of the individual amino acids the results for *E. × bidwillii* are also intermediate quantitatively (as measured by proportional representation).

OTHER SUBSTANCES

Once again, *Erythrina × bidwillii* shows an intermediate picture (Table 3). The test for lipids gave a negative result for nectars from all three taxa. Organic (reductive) acids were not detectable in *E. crista-galli* or the hybrid, but gave a strong reaction for *E. herbacea*. *Erythrina herbacea* and *E. × bidwillii* provided convincing evidence of the presence of phenolics while these were apparently only slightly represented in *E. crista-galli*. Proteins were not detectable in any of the nectars.

TABLE 3. Representations of various chemicals in nectars of two species of *Erythrina* and their hybrid.

Chemical	*E. crista-galli*	*E. × bidwillii*	*E. herbacea*
Lipids	N.D.[a]	N.D.[a]	N.D.[a]
Organic acids	Negative	Negative	Strong
Phenolics	Slight	Positive	Positive
Alkaloids	Negative	Negative	Positive
Proteins	N.D.[a]	N.D.[a]	N.D.[a]

[a] N.D. = not detected

Discussion

The results reported here refer to only one plant of each species. It can hardly be doubted that if a wider sampling of many populations of each species were undertaken (and it is our ambition to do this for the genus *Erythrina* as a whole) a greater amount of intraspecific variation might be revealed. However, the results are consistent with data that we have obtained from other investigations (Baker & Baker, 1976a, 1977).

There is intermediacy in the representation of the sugars in the hybrid and both quantitative intermediacy and qualitative additiveness in the amino acid complements.

Among the individual amino acids, the strengths of the amines, glutamine and asparagine, are notable, but the two "nonprotein" amino acids are probably the most important in their suggestion, being one in each species, that "nonprotein" amino acids in nectar could reveal taxonomic and phylogenetic information of value in studying the genus *Erythrina*. Certainly, there must be a wider investigation of nectar amino acids to see if there is merit to this suggestion.

It is interesting that the modest amount of information about the presence or absence of organic acids, phenolics and alkaloids suggests a greater degree of "chemical protection" against nectar-robbers in the nectar of *Erythrina herbacea* compared with *E. crista-galli*. Again, this is a promising area for investigation on a genus-wide basis.

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ASPECTS OF THE POLLINATION BIOLOGY OF THREE *ERYTHRINA* SPECIES ON TRINIDAD AND TOBAGO[1]

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ABSTRACT

Trinidad and Tobago support populations of three *Erythrina* species: *E. pallida*, *E. fusca*, and *E. poeppigiana*. We obtained data on visit frequencies of potential avian pollinators over two flowering seasons, as well as supplementary data on pollen loads, nectar secretion and availability, breeding systems, and extrafloral nectaries. These data show that *E. pallida* is pollinated exclusively by long-billed hummingbird species, whereas passerine birds are apparently more important than hummingbirds as pollen vectors of the large trees *E. poeppigiana* and *E. fusca*. Characteristics of flowers and nectar in the three species correlate with these contrasting modes of pollination. Inflorescences of all three species are protected from herbivores through extrafloral nectaries, which attract belligerent ants.

Trinidad and Tobago, politically in the West Indies but geographically and biologically an extension of South America, support populations of three *Erythrina* species. During a 14-month investigation of the ecology of nectar-feeding birds and bird-pollinated plants on these islands, we quantified frequencies of bird visits to flowers of each species and obtained supplemental data relevant to pollination biology. Below we present the results and attempt to integrate them into a comparative picture of the floral biology of these three species.

Tobago is smaller and biologically less diverse than Trinidad. Only 295 km^2 in area, Tobago is 42 km northeast of Trinidad, which is 4,540 km^2 in area and only 12 km from the South American mainland. Our Trinidad study sites (described below) supported 21 species of plants adapted for bird pollination, whereas on Tobago we found only 16 species (see also Beard, 1944, 1946). Trinidad contains 16 species of hummingbirds in total, Tobago only 6. The diversity of other bird species is also reduced on Tobago. Most of Tobago's biota, in fact, also occurs on Trinidad, so that we considered Trinidad as a "mainland" relative to Tobago.

Both islands hold the same assortment of *Erythrina* species. One is a recent import. *Erythrina poeppigiana* (Walpers) O. F. Cook was introduced from the lower slopes of the Venezuelan Andes in the 19th century (H. D. Adams, pers. comm.; B. A. Krukoff, pers. comm.). Planted as cacao shade on both islands, *E. poep-*

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[1] We thank Drs. B. A. Krukoff and P. H. Raven for inviting us to assemble our *Erythrina* data into a more or less coherent form. Dr. Krukoff, along with Dr. H. D. Adams, also helped to identify the *Erythrina* species, and provided information on their biology. Dr. G. Steyskal (U.S. National Museum) identified the fly on *E. fusca*, while S. Levings (Harvard University) determined the ant species. Dr. I. Baker spent considerable time analyzing the nectar samples, and we thank her and Dr. H. G. Baker for sharing an unpublished manuscript with us. Dr. D. Schemske volunteered information on the fly *Euxesta*. Our studies were supported by NSF grant DEB 76-20371 to Feinsinger, by a University of Florida Biomedical Research Support grant, and by institutional grants from the University of Colorado to Linhart.

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pigiana now reproduces naturally and has become the most common large tree in disturbed habitats. A mature individual, usually aphyllous at flowering, may hold up to 15,000 orange red flowers (illustrated in Krukoff & Barneby, 1974) at one time; flowers apparently last one day only. During the flowering peak of this species (see below), extensive areas on both islands, as seen from the air, seem entirely orange red; indeed, the boundary between orange red and green regions at that time of year demarcates the extent of past human disturbance.

Erythrina fusca Louriero, apparently native to both islands (B. A. Krukoff, pers. comm.), has also been replanted extensively for cacao shade. Natural reproduction occurs in wet soils such as those in lowland swamps or along streams, in contrast to *E. poeppigiana*, which grows on well-drained soils. Yellow orange flowers of *E. fusca* (illustrated in Krukoff & Barneby, 1974) last two days; if fertilization does not occur, flowers fall off during the second day. A single tree, usually aphyllous when flowering, may hold several thousand flowers. The flag of a flower must spring back to expose anthers and stigma. Apparently this action may occur spontaneously on the second day of flower maturity, but often pressure from foraging birds springs open a flower.

Erythrina pallida Britton & Rose is also native to both islands (B. A. Krukoff, pers. comm.; Krukoff & Barneby, 1974), where it is a small second-growth tree occasionally replanted as an ornamental or a "living fencepost." The pale rose-pink flowers last two days after anthesis; unfertilized flowers fall off late in the second day. Anthers and stigma are contained within the tubular flag, which must be penetrated at the distal end to obtain nectar. There are rarely more than a few dozen open flowers on a tree at any one time; trees we saw were always aphyllous at flowering. In short, the three *Erythrina* species exhibit two distinctive biologies. The two large, abundant tree species produce many conspicuous flowers, whereas the shrubby, uncommon *E. pallida* produces small numbers of less conspicuous flowers. The implications of this contrast to pollination biology are explored below.

METHODS

STUDY SITES AND VISIT SCHEDULES

During January, 1977, we set up 1,000 m of 20-m-wide transects in successional vegetation on each island, Trinidad and Tobago. The vegetation studied varied little within or between islands; both sites were at around 200 m elevation and faced similar climatic regimens. Floras at both sites, which had a dry season lasting from late December through early June, were also similar. Each site contained trees of all three *Erythrina* species; locations of trees were mapped. From February 1977 through 1 March 1978 we spent the first half of each month on Trinidad, the second half on Tobago. Below we term each two-week session a "time block."

FLOWER CENSUSES

On the first day of each time block, we counted the number of flowers on each bird-visited plant along the transects.

OBSERVATIONS

Each time block we spent the first six daylight hours (if few or no birds appeared) or the full 12-hour day observing and quantifying bird visits to a representative tree of each *Erythrina* species in flower. If some trees of *E. poeppigiana* or *E. fusca* possessed so many flowers that visit patterns differed from patterns at less fecund trees, we observed a representative low-density tree and a representative high-density tree. The subjectively determined cut-off point was ca. 300 flowers (*E. fusca*) or ca. 3,000 flowers (*E. poeppigiana*). For each bird visit to an observed tree, the following data were recorded: number of flowers visited, cumulative time spent probing flowers, direction of ingress and egress, aggressive interactions, and (qualitatively) frequency of contact with reproductive organs of flowers. From the number of open flowers on each tree observed, we calculated the mean frequency of probes per flower per day. To convert morning-only values to full-day values, for a given *Erythrina* species on each island we first determined the ratio of morning flower-probes to total flower-probes counted on those days having 12-hour observations; we then used this ratio to adjust 6-hour data to 12-hour estimates. We repeated this method on data for three distinct bird groups (see below): hummingbirds, bananaquits (*Coereba flaveola*), and all other bird visitors. Although data for hummingbirds should be accurate, we found it impossible to time flower-probes of passerine birds, which often foraged in large flocks, and also found it difficult to count accurately the number of flower-probes by passerines. Therefore, our data for birds other than hummingbirds are underestimates, if anything, of visit frequencies; this conservative bias should be consistent.

It has been suggested that *Erythrina fusca* is bat-pollinated (Helversen, cited in Raven, 1977). Therefore, during January and February, 1978, we spent two evenings, one on each island, watching for possible bat visitors to dense arrays of flowering *E. fusca*.

CONTROLLED POLLINATIONS

During February, 1978, we performed controlled pollinations on flowers of *Erythrina fusca* and *E. pallida* (there were no *E. poeppigiana* trees with accessible flowers). Pollinations occurred in early morning on days with no significant rain or wind. We handled anthers with forceps, which were cleansed with 95% ethanol between pollinations. Inflorescences were kept bagged before and after pollinations with three layers of cheesecloth (solid bags, for example Kraft bags or special "pollination bags," could not be used because temperature and humidity tended to rise inside them, causing all flowers to drop off). When necessary, cheesecloth bags were supported with sticks so as not to touch the flowers inside. Bags were so tightly closed that not even ants could enter (see below); on those occasions where by chance bags had opened at all, their flowers were not included in the data.

Only newly opened flowers in bagged inflorescences were used for pollen sources. Selfing was carried out with fresh pollen from the same flower: anthers were clipped off and one or more rubbed against the stigma until visible clumps

of pollen adhered. On Tobago, for *Erythrina pallida* we also used pollen from other flowers on the same tree; there was no differential effect. Cross-pollination was effected with freshly dehisced anthers from a bagged flower on another tree. Distances between trees used for cross-pollination varied from 20 m to 1 km. Because so few *E. fusca* flowers were within working distance of the ground, we did not perform cross-pollinations; instead, to determine if any self-compatibility existed, we performed only self-pollinations. We could obtain *E. pallida* data on both islands, but *E. fusca* data on Tobago only.

NECTAR AVAILABILITY

During each time block of January and February, 1978, we sampled nectar availability (standing crop) throughout the day in trees of *Erythrina poeppigiana* and *E. fusca* accessible to foraging birds (except that we could locate no reachable *E. poeppigiana* on Trinidad during January, 1978). Every two hours, from dawn through dusk, we clipped entire branches from the canopy with a pole pruner. Branches were carefully lowered to the ground so that nectar did not spill from the flowers. Each sample contained ten flowers, for each of which we determined nectar volume (with calibrated microcapillary tubes) and sugar concentration in g sucrose equivalents/100 g solution (with a temperature-compensated American Optical hand refractometer). Nectar samples were spotted on filter paper, dried, and sent to I. Baker and H. G. Baker at the University of California, Berkeley, for chemical analysis.

NECTAR SECRETION

On 24 February 1978 we investigated nectar secretion in the few accessible *Erythrina fusca* and *E. pallida* flowers on Tobago. Because flowers last two days, on the evening of the 22nd we had bagged with cheesecloth several flowers due to open on the 23rd; these were kept bagged through the 23rd, and on the evening of that day additional flowers due to open on the 24th were also bagged. On the 24th, the volume and sugar concentration of accumulated nectar in each flower were measured every two hours beginning at dawn.

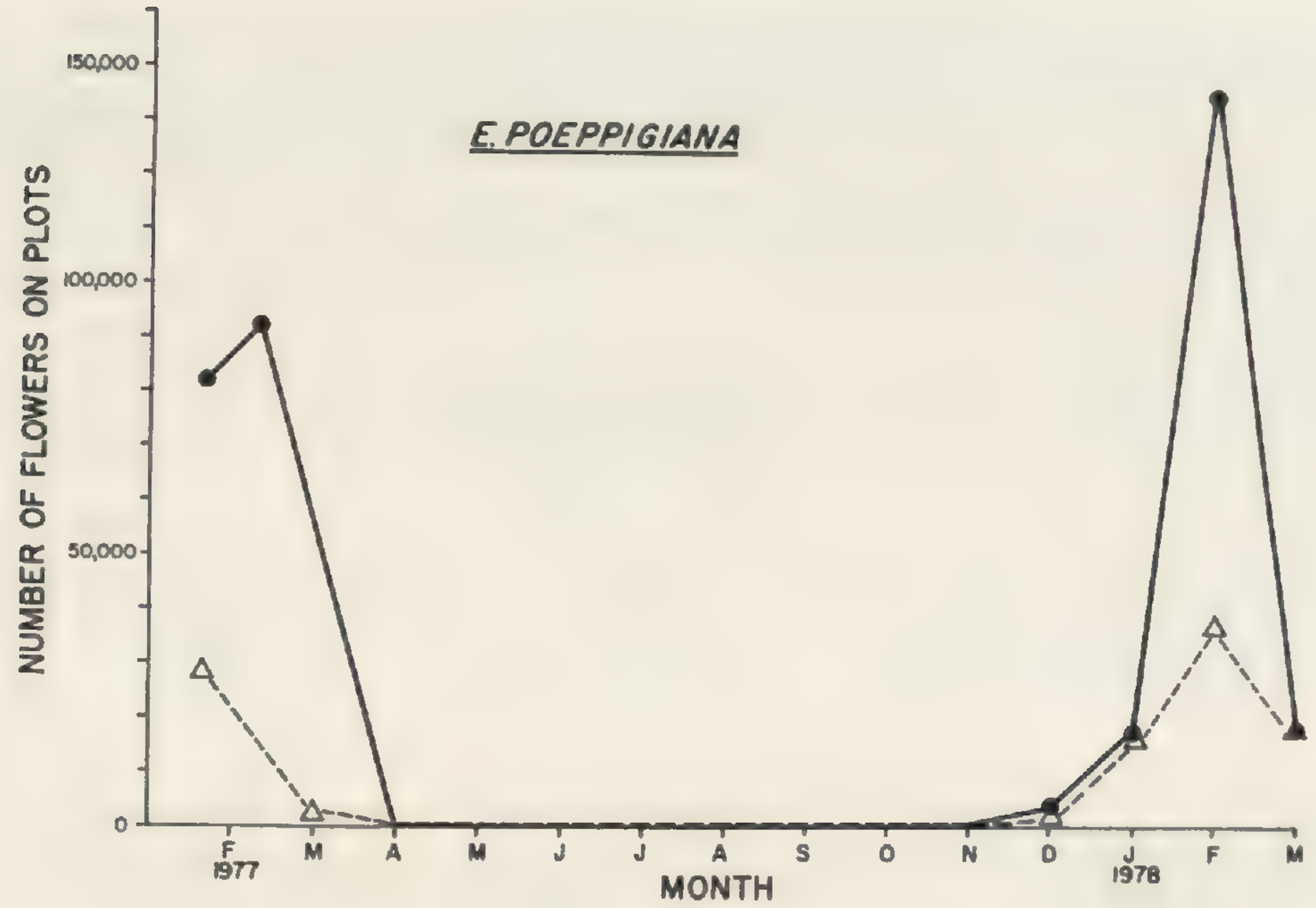
EXTRAFLORAL NECTARIES

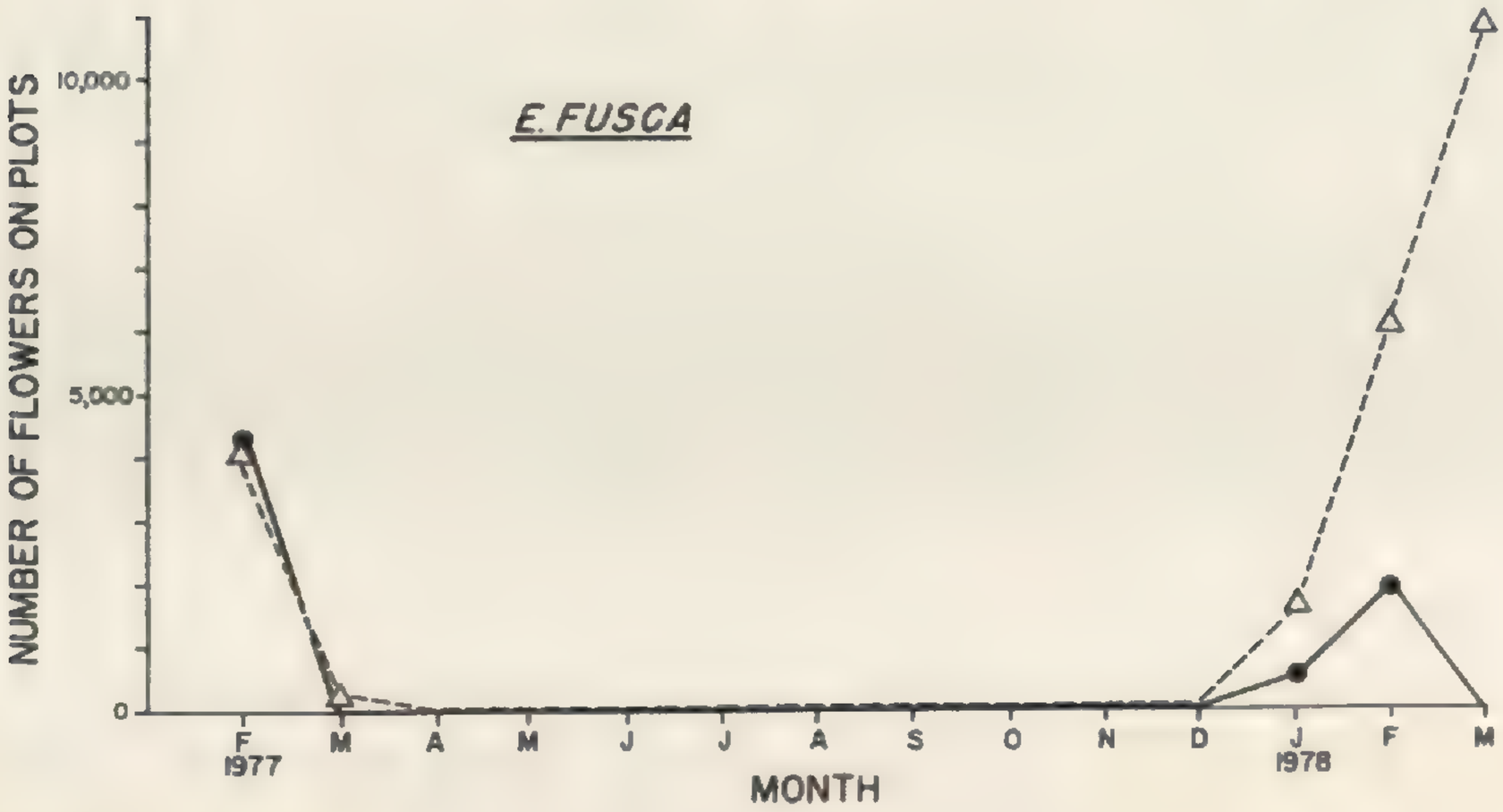
Careful examination of *Erythrina* flowers revealed protuberances on the ventral lip of each calyx. Protuberances were especially marked in buds (see illustrations in Krukoff & Barneby, 1974). The presence of ants at these protuberances suggested that they might be extrafloral nectaries (Bentley, 1977); therefore, we made observations on behavior of ants at these "bumps," and on "bumps" on inflorescences that had been bagged for other studies described above.

Results

FLOWERING PHENOLOGIES

Trinidad study plots contained 7 *Erythrina pallida*, 30 *E. poeppigiana*, and 5 *E. fusca* trees. Tobago plots contained 6 *E. pallida*, 15 *E. poeppigiana*, and


E. POEPPIGIANA
NUMBER OF FLOWERS ON PLOTS
150,000
100,000
50,000
0
F 1977
M
A
M
J
J
A
S
O
N
D
J 1978
F
M
MONTH


E. FUSCA
NUMBER OF FLOWERS ON PLOTS
10,000
5,000
0
F 1977
M
A
M
J
J
A
S
O
N
D
J 1978
F
M
MONTH

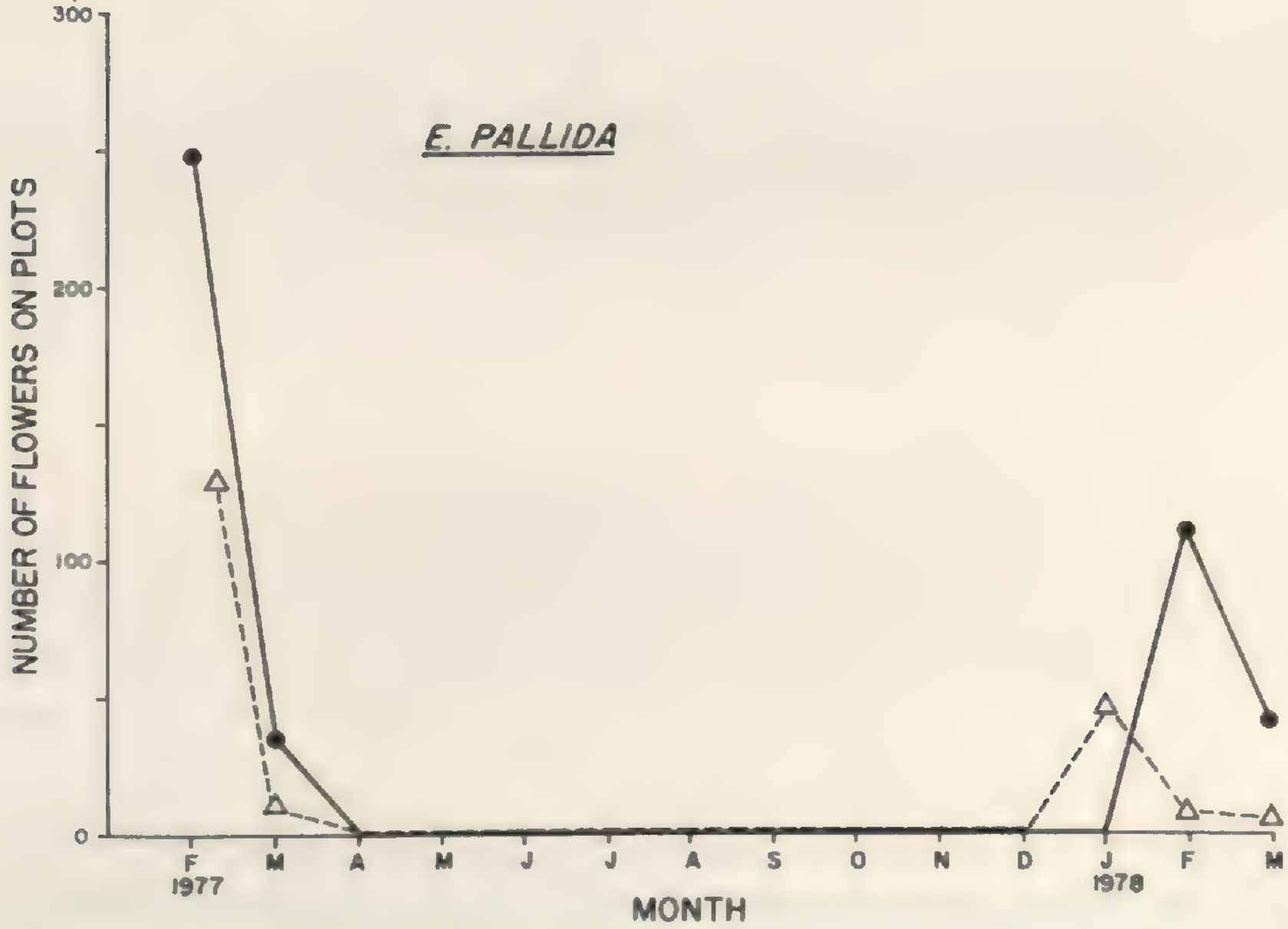

E. PALLIDA
NUMBER OF FLOWERS ON PLOTS
300
200
100
0
F 1977
M
A
M
J
J
A
S
O
N
D
J 1978
F
M
MONTH

TABLE 1. Results of controlled pollinations, performed as noted in text.

	Self-pollinated	Cross-pollinated
A. *Erythrina pallida*		
1. Trinidad		
Number of trees	4	4
Number of flowers	13	9
Flowers setting pods	2	1
Per cent pod-set	15%	11%
2. Tobago		
Number of trees	3	3
Number of flowers	83	33
Flowers setting pods	4	7
Per cent pod-set	5%	21%
B. *Erythrina fusca*, Tobago		
Number of trees	2	
Number of flowers	45	
Flowers setting pods	3	
Per cent pod-set	7%	

12 *E. fusca* trees. Flowering phenologies of all six populations are diagrammed in Fig. 1. The introduced *E. poeppigiana* had the least synchronized flowering; individual trees rarely flowered for more than two months, but because different trees were somewhat out of phase, the entire flowering season on each island lasted nearly five months, with a peak in February or March. *Erythrina fusca* flowered more synchronously, with a sharply defined February peak on each island and a total flowering season lasting less than three months. *Erythrina pallida*, which flowered for slightly over two months, peaked in January or February; there was slight asynchrony in the flowering seasons of individual trees.

CONTROLLED POLLINATIONS

The data in Table 1 suggest that both *Erythrina pallida* and *E. fusca* are not entirely self-incompatible. Our small samples indicate that pod-set for cross-pollinated *E. pallida* flowers does not greatly exceed pod-set for self-pollinated flowers. The results also suggest that selfing is possible in *E. fusca*. Pod-set from selfed flowers in both species exceeds the lower boundary that Bawa (1974) set for self-compatible trees.

VISIT FREQUENCIES

The data in Tables 2, 3, and 4 indicate that hummingbirds are the sole visitors to *Erythrina pallida*, whereas many bird species of diverse families visit the other two tree species. Both hummingbirds visiting *E. pallida* are "high-reward trap-

←

FIGURE 1. Flowering phenologies; numbers of flowers counted on consistent study plots, presented as two-month rolling averages. Solid line, circles: Trinidad. Dashed line, triangles: Tobago.

TABLE 2. Frequencies of bird visits to flowers of *Erythrina pallida*. Data from 12-hour observation days, or from 6-hour observations corrected as described in text. Mean over all flowers (last column) differs from mean over all days because different numbers of flowers were on different plants observed.

Island, Bird Species	Number of Days Seen	Total Flowers Visited	Visits / Flower / Day: Range	Mean Over All Observation Days	Mean Over All Flowers Observed
A. Trinidad					
Glaucis hirsuta	3	378	0–6.028	2.254	3.140
Heliomaster longirostris	3	313	0–2.813	1.332	1.704
Total hummingbirds	4/4	691	1.000–7.028	3.587	4.844
B. Tobago					
Glaucis hirsuta	2/4	67	0–13.000	4.620	4.360

liners" (Feinsinger & Colwell, 1978), or relatively large, long-billed hummingbirds that specialize on dispersed, nectar-rich flowers. Since they repeat throughout the day a foraging circuit that includes many different plant individuals, such birds are likely to be highly effective pollinators. In the Trinidad study area, we saw *Heliomaster* (which is absent from Tobago) consistently visit only one other plant species, which grew in more open habitats than *E. pallida*. *Glaucis hirsuta* individuals appeared to visit a wider variety of plants during foraging bouts. During 72 hours of observation, we observed no other flower visitors, bird or insect.

In contrast, only shorter-billed, opportunistic hummingbirds visited *Erythrina fusca* on either island (see Snow & Snow, 1972), and the accessible nectar in *E. fusca* blossoms attracted many other birds (Table 3). Even the conservative estimates for nonhummingbirds indicate that on Tobago, at least, hummingbirds visit flowers no more often than other birds, and that on Trinidad, also, birds other than hummingbirds visit many flowers. Data on *Coereba*, separated because this honeycreeper is much smaller and more nectarivorous than most other nonhummingbirds seen (Snow & Snow, 1971), suggest that it is not a conspicuous visitor to *E. fusca*.

At *Erythrina poeppigiana* (Table 4), however, *Coereba* visited flowers frequently (see Snow & Snow, 1971). The hummingbird visitors were similar to those at *E. fusca* but made many fewer visits per flower. Other birds spanned several families, but the frequency of any one species' visits was quite low.

We saw many bees and wasps hovering around the flowers of *Erythrina fusca* and *E. poeppigiana*. From our observation posts, we could not tell whether these entered flowers. We doubt that they were effective in pollination, since insects could easily have entered keels without contacting the reproductive parts. Many *E. poeppigiana* flowers on Tobago were pierced and the nectar removed. Although the holes may have been made by birds, they resembled holes bees chew in other flowers, so hymenopterans may remove nectar in this fashion without approaching the reproductive parts.

Table 3. Frequencies of bird visits to flowers of *Erythrina fusca*. Note that frequencies for birds other than hummingbirds are most likely underestimates (see text); visits by non-hummingbirds to high-density Tobago tree, February, 1977, were not counted at all because birds (especially *Thraupis episcopus*) were constantly in the tree in large numbers. See Table 2 for additional information.

Island, Bird Species	Number of Days Seen	Total Flowers Visited	Visits / Flower / Day: Range	Visits / Flower / Day: Mean Over All Observation Days	Visits / Flower / Day: Mean Over All Flowers Observed
A. Trinidad, low-density trees					
Hummingbirds:					
Chrysolampis mosquitus	2/2	190	0.345–0.587	0.466	0.544
Bananaquit:					
Coereba flaveola	1/2	9	0–0.047	0.024	0.039
Other birds (all Thraupidae):					
Tachyphonus rufus	2	23	0.023–0.168	0.096	0.049
Thraupis episcopus	1	12	0–0.143	0.072	0.025
Thraupis palmarum	1	17	0–0.043	0.022	0.035
Total other birds	2/2	52	0.066–0.311	0.188	0.109
B. Trinidad, high-density trees					
Hummingbirds:					
Chrysolampis mosquitus	2	6,635	1.015–1.169	1.092	1.088
Anthracothorax nigricollis	2	2,081	0.175–0.482	0.328	0.337
Amazilia chionopectus	2	223	0.014–0.056	0.035	0.036
Amazilia tobaci	2	440	0.052–0.091	0.072	0.073
Chlorestes notatus	2	242	0.006–0.082	0.044	0.042
Total hummingbirds	2/2	9,621	1.492–1.650	1.571	1.575
Bananaquit:					
Coereba flaveola	2/2	554	0.004–0.165	0.084	0.089
Other birds:					
Thraupidae:					
Thraupis episcopus	2	137	0.020–0.022	0.021	0.021
Thraupis palmarum	2	135	0.007–0.035	0.021	0.022
Tachyphonus rufus	2	418	0.025–0.109	0.067	0.065
Ramphocelus carbo	2	42	0.004–0.009	0.006	0.007
Icteridae:					
Icterus nigrogularis	1	5	0–0.002	0.001	0.001
Psarocolius decumanus	1	2	0–0.001	—	—
Fringillidae:					
Saltator coerulescens	1	14	0–0.004	0.002	0.002
Mixed passerines	1	88	0–0.026	0.013	0.014
Total passerines	2	841	0.122–0.142	0.132	0.131
C. Tobago, low-density trees					
Hummingbirds:					
Chrysolampis mosquitus	2	11	0–0.485	0.176	0.201
Anthracothorax nigricollis	2	19	0–0.791	0.213	0.219
Total hummingbirds	3/4	30	0–1.009	0.389	0.420

TABLE 3. *Continued.*

Island, Bird Species	Number of Days Seen	Total Flowers Visited	Visits / Flower / Day: Range	Visits / Flower / Day: Mean Over All Observation Days	Visits / Flower / Day: Mean Over All Flowers Observed
C. Tabago, low-density trees (*Continued*)					
Bananaquit:					
Coereba flaveola	2/4	44	0–0.511	0.132	0.159
Other birds:					
Thraupis episcopus (Thraupidae)	2	98	0–1.710	0.491	0.582
Mimus gilvus (Mimidae)	2	5	0–0.099	0.025	0.030
Melanerpes rubricapillus (Picidae)	1	5	0–0.045	0.021	0.023
Total other birds	2/2	108	0–1.847	0.537	0.635
D. Tobago, high-density trees					
Hummingbirds:					
Chrysolampis mosquitus	3	2,027	0.008–1.779	0.638	0.665
Anthracothorax nigricollis	2	346	0–0.354	0.121	0.113
Amazilia tobaci	1	6	0–0.006	0.002	0.002
Total hummingbirds	3/3	2,379	0.008–1.794	0.761	0.781
Bananaquit:					
Coereba flaveola	3/3	93	0.031–0.043	0.036	0.036
Other birds:					
Thraupidae:					
Thraupis episcopus	2	902	0.197–0.769	0.483	0.488
Tachyphonus rufus	2	7	0.002–0.013	0.008	0.007
Mimidae:					
Mimus gilvus	2	27	0.014–0.030	0.022	0.022
Icteridae:					
Psarocolius decumanus	1	16	0–0.015	0.008	0.008
Picidae:					
Melanerpes rubricapillus	1	2	0–0.002	0.001	0.001
Total other birds	2/2	954	0.240–0.802	0.521	0.526

Evening observations on *Erythrina fusca* trees provided no evidence for bat pollination. Although many bats, including potential flower-visitors, foraged on abundant mosquitoes in the swampy *E. fusca* habitat on both islands, we observed none to approach the flowers and heard no activity in the trees. The absence of claw marks or bite marks from fallen *E. fusca* flowers also indicated a lack of bat activity.

BEHAVIOR OF FLOWER VISITORS

Flower visitors do not necessarily transfer pollen (see Faegri & van der Pijl, 1971); thus values in Tables 2, 3, and 4 need not indicate the relative importance

of different birds in *Erythrina* pollination. Only on *E. pallida* did every visitor observed, *Glaucis hirsuta* or *Heliomaster longirostris*, consistently contact flower parts with its forehead or the base of its bill. Therefore, the values in Table 2 may well indicate the frequency of pollen deposition on *E. pallida* stigmas.

Hummingbirds were much less consistent at *Erythrina fusca* flowers. *Chrysolampis mosquitus*, the most frequent visitor, invariably probed beneath the enclosed anthers when visiting closed flowers (flowers whose flag had not sprung open). Only at occasional sprung flowers did foraging *Chrysolampis* brush against the reproductive parts. *Anthracothorax nigricollis* also brushed against anthers of sprung flowers on occasion, but most often missed the upthrust anthers entirely. At least *Anthracothorax* often moved between different *E. fusca* trees during foraging bouts, so that any pollen picked up might have been transferred, but often *Chrysolampis* remained in a single tree for long periods of time or flew from *E. fusca* to other plant species, so that any pollen picked up at one tree would rarely have been transferred to other *E. fusca*. Other birds, however, circulated among *E. fusca* trees in flocks. We often saw *Thraupis episcopus*, relatively large and strong foragers, spring open flowers, whereupon the released anthers struck them in the face or on the underside. We estimate that *T. episcopus* sprung about 10% of the closed flowers visited, and often brushed against the reproductive parts of open flowers with their undersides. *Tachyphonus rufus* appeared to spring closed flowers at a higher rate, ca. 25% of the time. Most other birds also fed in such ways that they sometimes sprung flowers or brushed against reproductive parts of open flowers. Small *Coereba flaveola* were rarely observed to spring a closed flower, but their heads or undersides often brushed against already sprung flowers in the act of feeding.

Since flags on *Erythrina poeppigiana* flowers evidently opened spontaneously when anthers matured, reproductive parts were always exposed, and birds feeding from the keel often brushed against the anthers or stigma with their undersides. Foraging hummingbirds such as *Chlorestes notatus* often appeared to touch the anthers. Large birds such as the Thraupidae often brushed against the anthers of one flower while feeding on another. Apparently, the most consistent pollinator was the bananaquit, *Coereba flaveola*, which nearly always contacted the reproductive parts either on its belly, chin, or (by perching behind a flower and tucking its head under) on its forehead or crown. Such unlikely visitors as woodpeckers, mockingbirds, and "seed-eating" grassquits often contacted reproductive parts, moved from tree to tree, and may have effected outcrossing. Parrots, which actually ate or dislodged flowers, were not likely to be especially effective pollen vectors.

POLLEN LOADS

Pollen loads collected from netted birds during the 1978 *Erythrina* flowering season confirm the observation data. Table 5 shows that *Glaucis hirsuta* on both islands carried many *E. pallida* pollen grains (unfortunately, no *Heliomaster* was netted during this period). Only three shorter-billed hummingbirds of ten examined carried any *Erythrina* pollen; on two this was clearly *E. poeppigiana* pollen. Four of eight *Coereba* carried *Erythrina* pollen; on one bird this was

TABLE 4. Frequencies of birds visits to flowers of *Erythrina poeppigiana*. Note that frequencies for birds other than hummingbirds are most likely underestimates (see text).

Island, Bird Species	Number of Days Seen	Total Flowers Visited	Visits / Flower / Day: Range	Visits / Flower / Day: Mean Over All Observation Days	Visits / Flower / Day: Mean Over All Flowers Observed
A. Trinidad, low-density trees					
Hummingbirds:					
Chlorestes notatus	2	224	0–1.130	0.208	0.102
Amazilia tobaci	3	149	0–0.673	0.113	0.067
Amazilia chionopectus	1	529	0–2.437	0.406	0.237
Anthracothorax nigricollis	3	124	0–0.396	0.209	0.067
Florisuga mellivora	1	2	0–0.009	0.002	0.001
Total hummingbirds	4/6	1,028	0–3.515	0.938	0.474
Bananaquit:					
Coereba flaveola	6/6	787	0.014–2.820	0.900	0.378
Other birds:					
Thraupidae:					
Thraupis episcopus	3	63	0–2.038	0.361	0.038
Thraupis palmarum	3	158	0–2.783	0.484	0.103
Tachyphonus rufus	2	36	0–0.161	0.040	0.017
Ramphocelus carbo	3	76	0–1.029	0.192	0.046
Icteridae:					
Icterus nigrogularis	1	39	0–0.180	0.030	0.018
Psarocolius decumanus	2	28	0–0.192	0.052	0.014
Picidae:					
Piculus rubiginosus	1	12	0–0.261	0.044	0.008
Total other birds	4/6	412	0–4.073	1.202	0.242
B. Trinidad, high-density trees					
Hummingbirds:					
Chlorestes notatus	4	2,444	0.001–0.314	0.109	0.076
Amazilia chionopectus	2	1,086	0–0.131	0.049	0.034
Amazilia tobaci	4	395	0.001–0.051	0.020	0.012
Anthracothorax nigricollis	4	532	0.001–0.080	0.022	0.017
Florisuga mellivora	2	23	0.001–0.002	0.001	0.001
Total hummingbirds	4/4	4,480	0.004–0.551	0.201	0.140
Bananaquit:					
Coereba flaveola	4/4	1,949	0.027–0.151	0.071	0.061
Other birds:					
Thraupidae:					
Thraupis episcopus	4	162	0.003–0.011	0.007	0.005
Thraupis palmarum	3	291	0–0.035	0.011	0.009
Tachyphonus rufus	4	89	0.001–0.010	0.004	0.003
Ramphocelus carbo	3	95	0–0.011	0.004	0.003
Tangara mexicana	1	8	—	—	—
Unidentified tanagers	2	174	0–0.027	0.008	0.005
Coerebidae (other than Bananaquit):					
Dacnis cayana	2	24	0–0.004	0.001	0.001
Icteridae:					
Icterus nigrogularis	2	21	0–0.001	—	—
Psarocolius decumanus	2	70	0–0.010	0.003	0.002
Cacicus cela	1	4	—	—	—
Scaphidura oryzivora	1	3	—	—	—

TABLE 4. *Continued.*

Island, Bird Species	Number of Days Seen	Total Flowers Visited	Visits / Flower / Day: Range	Visits / Flower / Day: Mean Over All Observation Days	Visits / Flower / Day: Mean Over All Flowers Observed
B. Trinidad, high-density trees (*Continued*)					
Vireonidae:					
Cyclarhis gujanensis	1	57	0–0.018	0.004	0.002
Fringillidae:					
Saltator coerulescens	1	4	—	—	—
Picidae:					
Piculus rubiginosis	1	12	0–0.001	—	—
Total other birds	4/4	1,014	0.011–0.095	0.043	0.032
C. Tobago, low-density trees					
Hummingbirds:					
Chrysolampis mosquitus	3	56	0–10.00	2.011	0.026
Amazilia tobaci	2	12	0–0.010	0.003	0.006
Anthracothorax nigricollis	1	32	0–0.033	0.007	0.015
Total hummingbirds	3/5	100	0–10.00	2.021	0.047
Bananaquit:					
Coereba flaveola	4/5	156	0–3.000	0.617	0.022
Other birds:					
Thraupidae:					
Thraupis episcopus	1	1	0–0.017	0.003	—
Tachyphonus rufus	3	24	0–0.183	0.041	0.008
Fringillidae:					
Tiaris bicolor	1	104	0–0.108	0.022	0.034
Mimidae:					
Mimus gilvus	1	1	0–0.001	—	—
Total passerines	3/5	130	0–0.200	0.066	0.042
D. Tobago, high-density trees					
Hummingbirds:					
Chrysolampis mosquitus	4	1,567	0.001–0.221	0.082	0.048
Anthracothorax nigricollis	2	277	0–0.020	0.010	0.008
Amazilia tobaci	2	42	0–0.043	0.012	0.002
Florisuga mellivora	1	766	0–1.154	0.288	0.023
Total hummingbirds	4/4	2,652	0.001–1.438	0.393	0.082
Bananaquit:					
Coereba flaveola	4/4	3,265	0.003–1.768	0.674	0.099
Other birds:					
Thraupidae:					
Thraupis episcopus	4	729	0.003–0.519	0.137	0.022
Tachyphonus rufus	4	166	0.001–0.025	0.009	0.005
Fringillidae:					
Tiaris bicolor	1	8	0–0.001	—	—
Mimidae:					
Mimus gilvus	4	151	0.001–0.023	0.011	0.007
Icteridae:					
Psarocolius decumanus	2	59	0–0.058	0.015	0.002
Picidae:					
Melanerpes rubricapillus	3	189	0–0.244	0.062	0.006
Veniliornis kirkii	1	15	0–0.022	0.006	0.001
Psittacidae:					
Amazona amazonica	2	383	0–0.218	0.059	0.011
Total other birds	4/4	1,700	0.026–1.101	0.298	0.051

TABLE 5. Pollen loads on birds mist-netted January and February, 1978. Number of pollen grains picked up by Scotch transparent tape (see text). If more than one bird of a given species was devoid of grains, the number of blank birds is given in parentheses.

	Number of Grains of			
Island, bird species	*E. pallida*	*E. poeppigiana*	*E. fusca*	Either *E. fusca* or *E. poeppigiana*
Trinidad:				
Hummingbirds:				
Glaucis hirsuta	135			
Glaucis hirsuta	1			
Glaucis hirsuta	33			
Amazilia tobaco (3)			—[a]	
Chlorestes notatus			—[a]	
Tobago:				
Hummingbirds:				
Glaucis hirsuta	763			
Glaucis hirsuta	990			
Glaucis hirsuta	330			
Glaucis hirsuta	8			
Glaucis hirsuta (2)			—[a]	
Amazilia tobaci			28	
Amazilia tobaci			12	
Amazilia tobaci (3)			—[a]	
Chrysolampis mosquitus				5
Bananaquits:				
Coereba flaveola				2
Coereba flaveola				1
Coereba flaveola				1
Coereba flaveola			2100	
Coereba flaveola (4)	—[a]			
Thraupidae:				
Thraupis episcopus				3
Thraupis episcopus				3
Thraupis episcopus			1	3
Thraupis episcopus				1
Thraupis episcopus			2	
Thraupis episcopus			2	
Thraupis episcopus	—[a]			
Tachyphonus rufus	3			1
Tachyphonus rufus	—[a]			

[a] Devoid of pollen grains.

identified as *E. fusca*. Of the fourteen larger tanagers examined, half carried either *E. fusca* or *E. poeppigiana* pollen. Observed loads were often small; birds may have originally carried larger loads that were lost during their frantic activity in the mist nets.

NECTAR SECRETION

Figure 2 shows that *Erythrina fusca* flowers secrete nectar during the day only (again arguing against bat pollination). Most secretion is on the first day.

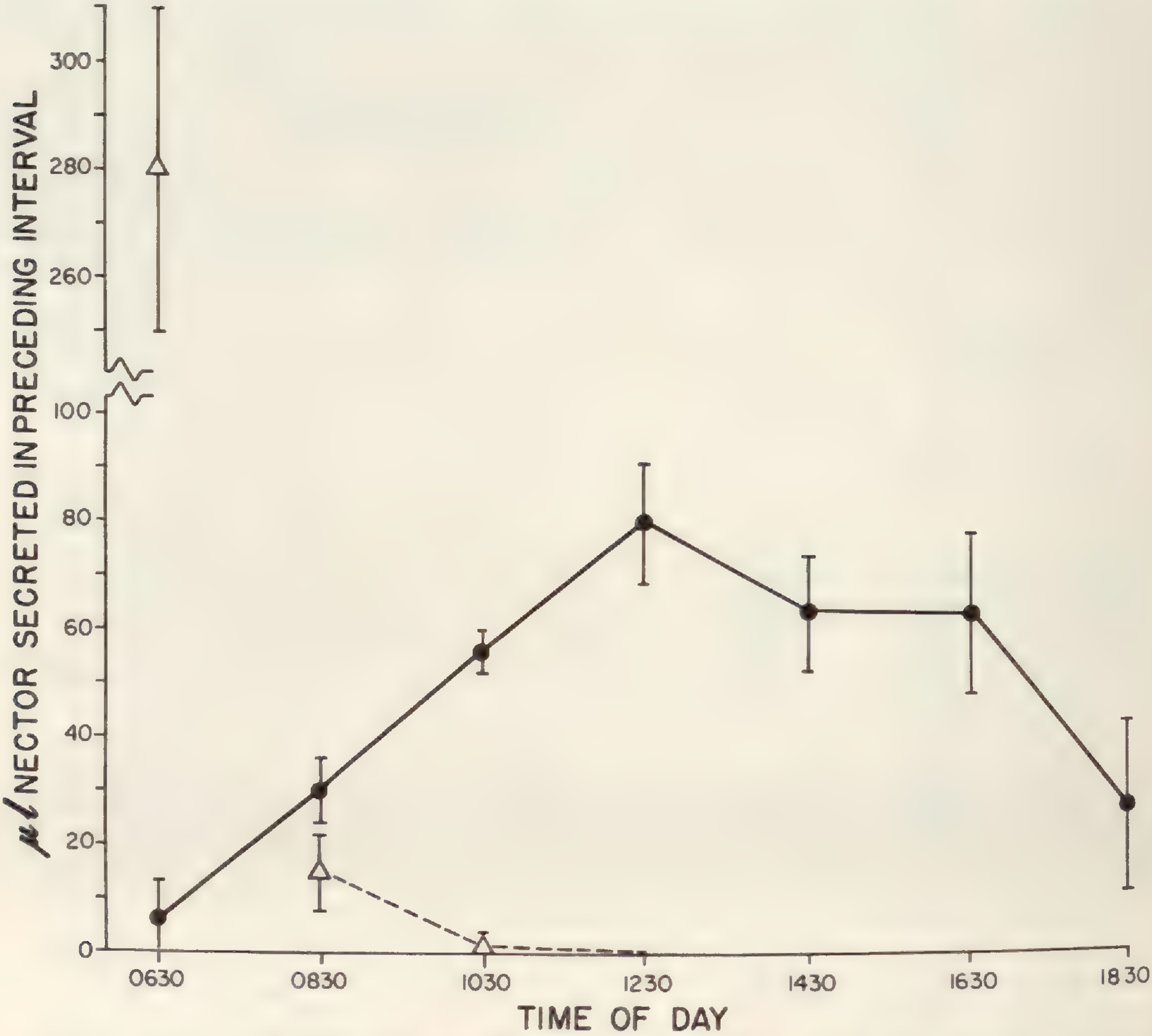


FIGURE 2. Nectar secretion in *Erythrina fusca* flowers. Solid line, circles: First-day flowers ($n = 5$). Dashed line, triangles: Second-day flowers ($n = 5$); so dawn value for second-day flowers is cumulative nectar from their first day of secretion. Mean ± one standard deviation.

The seven *E. pallida* flowers investigated secreted an average of 23.0 μl of nectar (s = 10.8 μl), with a sugar concentration of 29% in terms of g sucrose equivalence/100 g solution; day-old flowers secreted only trace amounts.

Erythrina fusca nectar analyzed by I. Baker and H. G. Baker (pers. comm.) had a higher concentration of monosaccharides than disaccharides: the ratio of sucrose to glucose + fructose was 0.038. The sucrose:glucose + fructose ratio for *E. poeppigiana* nectar was even lower (0.029). Both nectar samples contained many amino acids (see Baker & Baker, 1975); a complete list of tests performed is available from the authors or from I. Baker.

NECTAR AVAILABILITY

Copious secretion rates coupled with relatively infrequent bird visits left much nectar in flowers of *Erythrina fusca* and *E. poeppigiana* (Table 6). Even late in the day most flowers held large nectar volumes, up to 371 μl (concentration

TABLE 6. Nectar availability (standing crop) in flowers of *Erythrina* species exposed to foraging birds. Samples of 10 flowers.

A. Trinidad

1. January 16, 1978. *Erythrina fusca* only.

Time	Mean vol., μl	s	Number with ⩽10 μl
0615	135.0	88.4	0
0815	125.2	23.8	0
1015	117.1	66.8	2
1215	126.2	75.3	2
1415	108.7	86.5	3
1615	124.3	109.0	1
1745	124.5	55.6	0

Mean sugar concentration: 18.0% (s = 1.3%)

2. February 3, 1978

Time	Mean vol., μl	s	Number with ⩽10 μl	Mean vol., μl	s	Number with ⩽10 μl
	Erythrina fusca			*Erythrina poeppigiana*		
0615	109.9	70.2	0	21.9	27.3	5
0815	108.8	60.3	1	50.0	33.3	1
1015	138.4	109.3	1	14.2	27.5	7
1215	109.4	69.1	1	19.5	16.5	4
1415	120.6	84.3	0	80.8	60.8	1
1615	75.7	83.3	2	49.6	37.2	0
1715	95.5	75.7	3	32.7	31.4	4
Mean sugar concentration:	19.7% (s = 4.2%)			17.6% (s = 1.5%)		

16.5 g sucrose equivalence/100 g solution) in *E. fusca* and up to 254.7 μl (16.5 g sucrose equivalence/100 g solution) in *E. poeppigiana*. In February, many *E. poeppigiana* flowers on both islands held less than 10 μl. Observed bird visits were less frequent in February than in January, however. Possibly the hillside soils upon which *E. poeppigiana* trees grew were so dry that nectar secretion was inhibited. It is also possible that insect visits had increased by this time; we noted that many flowers on the Tobago trees had been pierced as described above.

EXTRAFLORAL NECTARIES

For at least *Erythrina fusca* and *E. pallida*, we demonstrated protuberances on the calyces to function as extrafloral nectaries when we bagged inflorescences for controlled pollination studies. Figure 3 shows the results: the protuberances of both species, protected from foraging ants, secreted conspicuous, glistening droplets of nectar. Exposed nectaries on both species attracted many ants (e.g., Fig. 3d). We collected numerous *Cephalotes atratus* from Tobago *E. fusca*, and *Ectotomma tuberculatum*, *Monacis valida*, and *Camponotis* sp. from Tobago *E. pallida* nectaries. On Trinidad, we also noted *Ectotomma ruidum* and *Was-*

TABLE 6. *Continued.*

B. Tobago

1. January 23, 1978

Time	Mean vol., μl	s	Number with ⩽10 μl	Mean vol., μl	s	Number with ⩽10 μl
	Erythrina fusca			*Erythrina poeppigiana*		
0625	169.1	118.6	0	139.0	40.4	0
0815	166.8	81.8	0	116.5	49.9	0
1015	154.1	77.6	0	123.6	58.1	0
1215	172.3	96.0	0	109.2	85.4	0
1430	251.9	20.4	0	141.0	81.1	1
1615	198.2	63.7	0	120.2	85.3	1
1720	194.3	122.7	2	129.1	103.3	2
Mean sugar concentration:	16.8% (s = 1.0%)			16.8% (s = 0.7%)		

2. February 24, 1978

Time	Mean vol., μl	s	Number with ⩽10 μl	Mean vol., μl	s	Number with ⩽10 μl
	Erythrina fusca			*Erythrina poeppigiana*		
0615	17.3	41.7	9	4.1	6.2	8
0815	70.9	83.6	3	31.0	18.1	2
1015	89.7	78.4	0	31.5	32.1	4
1215	62.5	33.6	1	9.7	13.4	7
1415	100.1	59.0	1	6.5	12.6	7
1615	116.5	81.6	1	5.6	11.4	8
1745	105.8	72.0	1	19.2	20.9	4
Mean sugar concentration:	13.4% (s = 2.9%)			15.5% (s = 2.7%)		

mannia auropunctata at *E. fusca* nectaries and on *E. poeppigiana* as well (see Feinsinger & Swarm, 1978). All species acted aggressively towards human manipulation of flowers, moving quickly towards the source of disturbance with mandibles open (*Cephalotes*, *Ectotomma*, *Camponotis*) or stinging (*Wasmannia*). Bentley (1977) cites the genus *Ectotomma* as a common "pugnacious bodyguard" associated with extrafloral nectaries on tropical plants. To our knowledge the only other description of extrafloral nectaries on *Erythrina* is by Mattei (1925; cited in Bentley, 1977).

The function of extrafloral nectaries and their attendant ants was graphically illustrated on two Tobago *Erythrina fusca* trees. On Tree A, which grew in typical *E. fusca* habitat near a stream, extrafloral nectaries on bagged inflorescences secreted abundant nectar (e.g., Fig. 3a), and unbagged inflorescences on the tree were full of roving, aggressive ants. There was no visible predation on this tree's flowers. Tree B grew on a dry hillside some 20 m from the stream and was investigated on the same days as Tree A. Inflorescences bagged for controlled pollinations secreted no visible extrafloral nectar. This contrast between the two trees' nectaries was observed for three consecutive days. We saw

FIGURE 3. Extrafloral nectaries on calyces.—a. *Erythrina fusca* buds protected from ants for 12 hours.—b. *E. pallida* buds protected from ants for 12 hours.—c. *E. pallida* flowers protected from ants for 12 hours.—d. Unidentified ant foraging at nectary on *E. pallida* bud.

no ants on Tree B. Several inflorescences on Tree B were rendered into pulpy masses by an unidentified lepidopteran larva (Fig. 4a). Many flowers in other inflorescences had been attacked by flies of a previously undescribed species in the genus *Euxesta* (family Otitidae), whose larvae bore through the flower and doubtlessly reduce its reproductive potential (Fig. 4b). During the same period (late February, 1978) we repeatedly observed *Euxesta*, of a species similar to that of *E. fusca*, active around inflorescences of Tobago *E. pallida*. These flies often landed on *E. pallida* buds and flowers, but invariably fled as attendant ants moved towards them. Other species of *Euxesta* are important parasites of inflorescences of *Costus* (Zingiberaceae) in Panama (D. Schemske, pers. comm.).

DISCUSSION

MODES OF POLLINATION

Erythrina pallida.—The floral biology of *E. pallida* is a straight-forward case of hummingbird pollination. Data on flower visitors (Table 3) and pollen loads (Table 5) demonstrate that long-billed hummingbirds functioned as effective pollinators at our study sites. Nectar flow rates were low relative to the other two *Erythrina* species, as Cruden & Toledo (1977) discovered for hummingbird-pollinated *Erythrina* species in Mexico; yet nectar secretion and sugar concentration were sufficiently high to support large hummingbirds rather than the

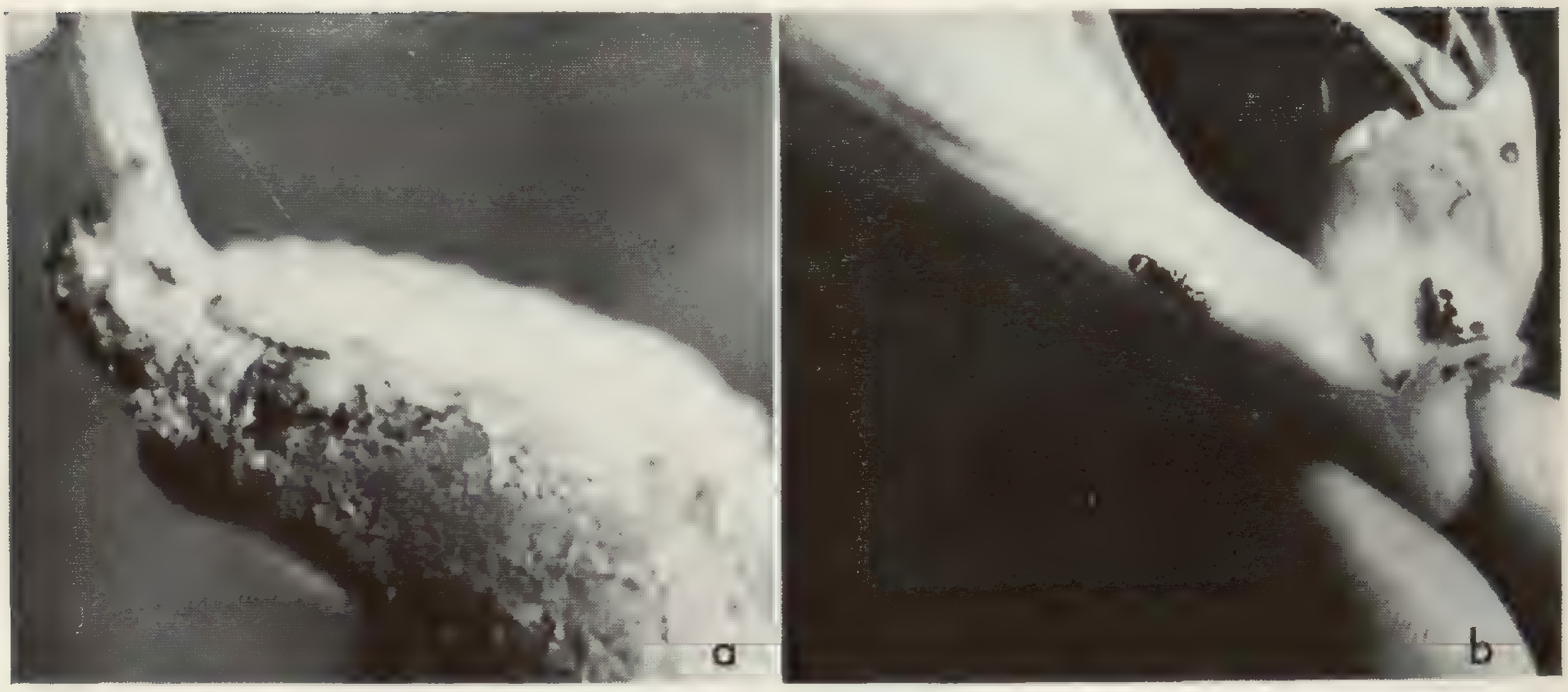


FIGURE 4. Damage to an *Erythrina fusca* tree whose extrafloral nectaries did not secrete nectar (see text).—a. Entire inflorescence rendered into pulpy mass by unidentified lepidopteran larvae.—b. Larval exit hole (round orifice), larval feces (black masses), and adult of fly *Euxesta* sp. on individual flower.

smaller, shorter-billed species (see Bolten & Feinsinger, 1978; Feinsinger & Colwell, 1978). Apparently, *E. pallida* flowers have thus evolved to utilize long-billed hummingbirds as pollen vectors such that hummingbirds are the only means by which outbreeding may be effected (see Raven, 1974, 1977). Anthers and stigma are in close proximity, however. Data from controlled pollination studies (Table 1) suggest that in the absence of hummingbirds fertilization might still occur through autogamy. Pods set per flower appeared to be quite high, at least 10% on Trinidad.

Erythrina fusca.—*E. fusca* contrasts with *E. pallida* in nearly every facet of floral biology. The easily obtained, copious nectar is typical of many *Erythrina* species pollinated by passerine birds (see Raven, 1974, 1977; Cruden & Toledo, 1977). Although bat flowers also secrete copious nectar (Heinrich & Raven, 1972), the diurnal nectar secretion pattern and lack of observed bat visits suggest that bats are not important in the floral biology of Trinidad and Tobago *E. fusca*, although they may act as pollinators of Colombian populations (Helversen, cited in Raven, 1977). The pollen loads we obtained from mist-netted birds are not conclusive, but it is evident that passerine birds are capable of carrying *E. fusca* pollen and acting as outbreeding agents. Tanagers appear to be especially important in springing flowers and transferring pollen. Only on occasion do hummingbirds (which frequently visit flowers but rarely contact reproductive parts) or bananaquits (which rarely visit flowers although during visits they frequently contact reproductive parts on sprung flowers) assume importance in pollen transfer. The low sucrose:glucose + fructose ratio typifies passerine-pollinated plants throughout the tropics (Cruden & Toledo, 1977; Baker & Baker, 1980). The copious nectar left in flowers at the end of the day suggests that not all flowers receive bird visits; our sparse data on controlled pollinations, coupled with the observation that anthers and stigma are adjacent to one another, suggest that autogamy is possible. Qualitative observations on fruiting trees indicate that only a small fraction of flowers (fewer than 1%) results in mature pods.

Erythrina poeppigiana.—Like *E. fusca*, *E. poeppigiana* appears to be adapted for pollination by passerine birds. Nectar availability (and doubtless secretion rates), while lower than in *E. fusca* (Table 6), far exceed secretion rates in *E. pallida* or most other hummingbird-pollinated plants with which we are familiar. Again, the low disaccharide:monosaccharide ratio suggests passerine pollination (Baker & Baker, 1980). Data on pollen loads corroborate our observations that passerine birds (particularly *Coereba flaveola*), as well as occasional hummingbirds, can act as pollen vectors. Patterns on Trinidad and Tobago may not be representative of floral biology in native Venezuelan populations of *E. poeppigiana*; however, *Coereba flaveola* is apparently abundant throughout *E. poeppigiana*'s natural range (Krukoff & Barneby, 1974; Schauensee & Phelps, 1978). Although we could not obtain data on breeding systems in this species, the spread of feral trees on both islands argues that fertilization often occurs, whether by allogamy or autogamy. Nevertheless, pod-set is apparently quite low; most trees produced large seed crops, but the number of pods set appeared to be less than 1% of the total number of flowers each tree produced over its flowering season.

ISLAND EFFECTS ON FLORAL BIOLOGY

In another comparison of bird pollination on Trinidad and Tobago, Linhart & Feinsinger (in press) showed that life on a small island (Tobago) affected a plant species specialized for pollination by long-billed hummingbirds much more than a plant species with open flowers acceptable to a variety of birds. The contrast between the three *Erythrina* species is similar. *Erythrina pallida* was visited by two hummingbirds on Trinidad, one of which was a virtual specialist on the plant. Every observed plant was visited by one or both species. On Tobago, *E. pallida* received no visits whatsoever on two of four observation days. Its sole visitor on Tobago, the hummingbird *Glaucis hirsuta*, visited many other plant species during its foraging bouts, so that pollen may have been lost between successive visits to different *E. pallida* individuals. Therefore, it is likely that outbreeding was much more consistent among Trinidad than Tobago plants.

Although hummingbird visit frequencies to *Erythrina fusca* flowers were also higher on Trinidad than on Tobago, the reverse was true for other birds (Table 3), particularly *Thraupis episcopus*. These tanagers are much more dense on Tobago than Trinidad, so that the increase in visit frequencies (and possibly increased outbreeding) among Tobago *E. fusca* is an interesting consequence of "density compensation" in this island bird population (cf. Diamond, 1970; MacArthur et al., 1972). An important pollinator of *E. poeppigiana*, *Coereba flaveola*, is also much more frequent on Tobago than Trinidad, and its visits to large *E. poeppigiana* trees are consequently more frequent on Tobago. Our circumstantial evidence suggests that, in contrast to *E. pallida*, neither of the large-flowered, generalized *Erythrina* tree species suffered a considerable decrease in outbreeding in the transition from mainlandlike Trinidad to the small island Tobago.

CONCLUSIONS

Flowering in all three *Erythrina* species occurs at a time when most individuals have shed their leaves and photosynthesis is unlikely. The profligate use of

flowers and nectar in the two large tree species, at least, must constitute a considerable energy drain; we noted that only exceptionally large, healthy trees produced large flower crops. Copious nectar secretion may be necessary to attract passerine pollinators (cf. Cruden & Toledo, 1977); whether dense flower crops are another adaptation for attracting passerines, or whether passerines are especially adaptive for bird-pollinated plants with dense flower crops because flocking passerines respond to increased flower density more linearly than aggressive, territorial hummingbirds (cf. Feinsinger, 1978), is open to speculation. In either case, a smaller, dispersed plant species not capable of producing large flower crops, such as *E. pallida*, would be unlikely to benefit from visits by opportunistic passerines. Specialized, flower-specific hummingbirds are doubtless most effective in dispersing pollen among conspecifics, indicated by relatively frequent pod-set, although on a small island such as Tobago there is a danger of even hummingbirds becoming inconstant. In light of the energy all three species invest in reproduction, it is significant that inflorescences are protected by means of extrafloral nectaries, which function to attract pugnacious ants. Floral nectar, which must be left available to potential pollinators, can also attract ants when removed from the flower (Feinsinger & Swarm, 1978), but the waxy inner surface of flowers appears to deter ants from floral nectar. Thus functions of the two spatially proximate nectaries are kept separate. Finally, water stress may affect secretion by either type of nectary. Lack of nectar in extrafloral nectaries may increase predation on flowers, as shown for *E. fusca*, whereas low nectar secretion by floral nectaries may discourage birds from visiting trees, as proposed for *E. poeppigiana*. Thus water stress could exert selective pressure on flowering phenologies and habitat preferences of all three species.

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ANT-VISITED EXTRAFLORAL (CALYX AND FOLIAR) NECTARIES AND NECTAR SUGARS OF *ERYTHRINA FLABELLIFORMIS* KEARNEY IN ARIZONA[1]

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ABSTRACT

Extrafloral glands are noted on calyces of floral buds, before and during anthesis, and on petiolar stipels at early and later stages of leaf development. Liquid chromatographic sugar analysis of extrafloral and floral nectars shows that the extrafloral nectars (calyx and foliar) are fructose-glucose dominant while the floral nectar is sucrose dominant. Seven species of ants were noted visiting temporally separated calyx and foliar extrafloral nectaries, suggesting a possible myrmecophilous role.

Mattei's early (1925) report of extrafloral nectaries, to which he attributed a myrmecophilous role, on the calyces and leaf petioles of *Erythrina tomentosa* R. Brown ex A. Richard (= *E. abyssinica* Lamarck ex A. DC.; Krukoff & Barneby, 1974) and on the calyces of *E. hastifolia* Bertoloni (= *E. humeana* Sprengel; Krukoff & Barneby, 1974) has been overlooked in the literature on the genus. Apparently until recently no other species in this large and widespread tropical genus has been noted to have extrafloral nectaries or to be myrmecophilous. Feinsinger & Swarm (1978) note ant use of extrafloral nectaries on *E. poeppigiana* (Walpers) O. F. Cook and *E. fusca* Loureiro in Trinidad and Feinsinger et al. (this symposium) describe ant visitation of extrafloral-calyx glands on *E. fusca* and *E. pallida* Britton & Rose. Kearney (1894) made no mention of extrafloral nectaries in his description of *E. flabelliformis*. But in the since synonymized description of the same species from Baja California as *E. purpusi*, Brandegee (1903) described the calyx as "bearing a large gland on the lower lip."

Our study was initiated after preliminary observations during the summer of 1977 indicated that ants were visiting two types of extrafloral nectaries on *Erythrina flabelliformis* in southern Arizona. The purpose of this report is to describe the presence of calyx and foliar extrafloral nectaries on *E. flabelliformis*; to establish that the extrafloral nectaries produce sugars; to compare the relative proportions of glucose, fructose and sucrose in the extrafloral nectars and in the floral nectar; and to note the visitation of extrafloral nectaries by ants.

Raven (1974, 1977, this symposium) has reviewed knowledge on the biology

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[1] James E. Ambrose, Jr. translated several points in Mattei's 1925 paper and gave permission to study *Erythrina* on his land, Ráfagas. Susan Kunz volunteered assistance in the field. James W. Berry and Charles W. Weber generously allowed J.C.S. use of their laboratory and equipment for the analysis of nectar sugars. Floyd G. Werner helped with preliminary identifications of ants. Roy R. Snelling, Los Angeles County Museum of Natural History, provided the final determinations of ant species utilized in the text. Charles H. Pickett, Peter Feinsinger, Herbert G. Baker, and Irene Baker provided us with copies of unpublished manuscripts. Herbert G. Baker and Jean L. Mills gave valuable criticisms of the manuscript. We thank all of the above for their contributions.

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of the genus *Erythrina* in introductory papers to the *Erythrina* symposia. It is a very distinct genus of Fabaceae consisting of 108 species of trees, shrubs, and a few herbs of wide distribution primarily in the tropics. Two species are native to the United States. *Erythrina flabelliformis* grows as a shrub on rocky outcrops in Arizona at the northern extent of its range (Conn, 1976); farther south in Mexico it attains tree form (Gentry, 1942). In Arizona *Erythrina* shrubs are dormant from fall until late spring. Kearney & Peebles (1960) note that the "flowers appear mainly in spring before the leaves" and Krukoff (1939) states that it is "aphyllous or rarely with young leaves at anthesis." Leafing appears to be in response to summer rains (Conn, 1976) and plants remain in leaf for approximately six weeks (Krukoff, 1939).

Narrow, tubularlike, hummingbird-pollinated flowers have evolved in New World species of *Erythrina* (Toledo, 1974; Raven, 1977) and *E. flabelliformis* is visited by hummingbirds in southern Arizona (Grant & Grant, 1968; Conn, 1976): including the black-chinned hummingbird, *Archilochus alexandri* (personal observation W.C.S.).

Methods

Two Arizona populations, designated Molino Basin and Ráfagas, were utilized for this study. The first is located at 1,430 m elevation in Molino Canyon of the Santa Catalina Mountains (same population as studied by Conn, 1976). The second population is located in a box canyon (center of section 13, T17S, R23E, Pearce Quadrangle) approximately 1.6 km north of the entrance to Stronghold Canyon East at 1,520 m elevation in the Dragoon Mountains. During 1978 one or both of us visited Molino Basin twelve times and Ráfagas twice.

Ten shrubs were tagged at each locality and their locations were mapped to allow repeated collection throughout the season of various nectars (floral, extrafloral-calyx, and extrafloral-foliar) and ants from identified plants. Samples of floral nectar were easily obtained from all plants at both localities early in the season. Samples of extrafloral nectar were difficult to obtain as the quantities of nectar accumulated at the glands were small, usually not easily visible to the naked eye. Nevertheless, they were visited by ants (Figs. 1B, 1D). Only two plants provided sufficiently large samples of extrafloral-calyx nectar, and only one of extrafloral-foliar nectar, for collection and analysis. All three were Molino Basin plants.

Floral nectar was collected at Molino Basin on June 4 (3 plants) and June 18 (7 plants) and at Ráfagas on June 11 (10 plants). Extrafloral-calyx nectar was collected at Molino Basin on June 4 (3 plants; encrusted nectar) and June 18 (2 plants; clear, viscous fluid). Fifty additional plants at this locality were examined on June 22, but none contained sufficient quantities of extrafloral-calyx nectar for collection. In unsuccessful efforts to obtain samples of nectar from extrafloral-foliar nectaries, tagged plants at Molino Basin were visited eight times between July 16 and September 7; one sufficiently abundant extrafloral-foliar nectar sample was obtained at this locality on August 15 (1 plant; clear, viscous fluid).

Floral nectar was collected at anthesis from approximately 10 to 20 flowers as each was removed from an individual plant. The three samples collected on June 4 were obtained by breaking off the banner petal near its base and then lightly squeezing the calyx tube. This caused a nectar droplet to well up from the calyx tube at its upper lip near or between the wing petals. This nectar was taken up with a 50 μl syringe, care being taken to avoid the region of the extrafloral gland on the lower lip of the calyx, and deposited in a vial with 80% ethanol. The pinkish, slightly-viscous nectar from these first three samples was later thought to be possibly contaminated by fluids from the ruptured banner petal. Subsequent samples of floral nectar (June 11, 18) were made in an identical manner except that the banner petal was plucked off at its natural juncture with the ovary wall. The resulting nectar droplet was clear in color, suggesting that earlier pinkish samples contained some petal fluids; June 4 samples were not included in the Molino Basin floral nectar analysis.

On June 4 extrafloral-calyx nectar that had apparently dried and become encrusted was removed from the orifices of glands on three plants and placed in 80% ethanol. This material failed to dissolve completely and when analyzed only two samples gave results of sugars. On June 18 two plants were found to have unusually large droplets of sticky, clear nectar balled-up on the surface of the extrafloral-calyx nectaries (Fig. 1A). This very viscous material was removed from buds of each plant by adhering it to the point of a syringe and then transferring it into 80% ethanol in collection vials where it dissolved readily.

On August 15 a sample of extrafloral-foliar nectar was collected in a similar manner from approximately 30 pairs of stipellate glands on leaf petioles of one plant. Ants had been excluded from selected branches of this and several other plants since August 2 by encircling the stem with Vaseline™ petroleum jelly. (Ant exclusion seemed to facilitate the accumulation of nectar at extrafloral-foliar glands, Fig. 1C, but the technique did not increase the nectar accumulation on every plant so treated.)

On August 2 the position and number of extrafloral-foliar glands on the petioles of ten mature leaves of each of the ten tagged plants at Molino Basin were recorded.

All nectar samples were dissolved at the site in 80% ethanol, and later concentrated for chromatographic analyses by solvent evaporation in a nitrogen stream. Analyses were performed by direct injection of samples on a Waters™ model ALC/GPC 244 High Pressure Liquid Chromatograph equipped with a differential refractometer. Samples were eluted from a μCarbohydrate™ (reverse phase) column under the following conditions: solvent—80:20 acetonitrile:water (isocratic elution); and flow rate—2.0 ml/min. The sugars were identified against standards by their retention times. Their relative concentrations were calculated by triangulation of peak areas and are reported as percentages of total sugars. (Note: standards of glucose, fructose and sucrose yield similar detector response versus concentration curves.)

It was beyond the scope of this study to relate chromatographic analyses to total sugar concentration within nectars. Total sugar concentration is subject to

FIGURE 1. Extrafloral (calyx and foliar) nectaries of *Erythrina flabelliformis*.—A. An unusually abundant concentration of clear, viscous droplets of extrafloral nectar on bud calyces.—B. *Camponotus ulcerosus* Wheeler (in circle) visiting an extrafloral-calyx nectary on an unopened floral bud (black arrows point to extrafloral calyx glands; white arrows point to emerging corollas of lower buds).—C. Extrafloral-foliar nectar concentrations (on ant-excluded plant) at openings in paired stipellate glands at the bases of secondary leaflets.—D. *Pseudomyrmex pallidus* F. Smith visiting one of a pair of extrafloral-foliar nectaries on an immature leaf (arrows point to enlarged glands on a younger leaf).

environmental changes, and its measurement requires large amounts of nectar collected under exacting conditions (Baker & Baker, 1975).

Samples of ant species found visiting either calyx or foliar extrafloral nectaries at both localities were collected during daylight hours and preserved in 80% ethanol. An effort was made to collect examples of all species foraging on each plant. Seven plants at Molino Basin were surveyed at least twice during the

season to determine if the same species of ants were visiting both calyx and foliar extrafloral nectaries of individual plants.

RESULTS AND DISCUSSION

In 1978 approximately half of the leafless plants at Molino Basin were in bloom on June 4, many of the remainder had developing inflorescences. By June 22 few floral buds remained, and on July 16 flowering had almost terminated and plants were developing leaves and seed pods. Later, on September 17, leaves were changing color. Thus the blooming period in 1978 was roughly one and a half months, and plants were in leaf during approximately the following two months. This phenological sequence agrees with the more detailed phenological data reported for the same site in 1975 by Conn (1976).

Two types of extrafloral nectaries were identified in *Erythrina flabelliformis*. An extrafloral-calyx nectary occurs on the lower lip, just below the corolla, of each grayish, pubescent calyx. This nectary is clearly evident on floral buds well before the scarlet red corolla appears, and the nectary remains obvious as a bright green, protruding, glandular structure throughout anthesis (Fig. 1B). The paired extrafloral-foliar nectaries are located on the ternate compound leaves on either side of the upper surface of the petiole, proximal to the attachment of the secondary leaflets (Fig. 1C). All 100 leaves surveyed had this pair of nectaries; three leaves had an additional pair on the petiole near the base of the terminal leaflet; and one had a single nectary in this position. Nectar is secreted via a horizontal orifice always located on the stem side of these modified, usually ovular, but sometimes pointed, stipels (Fig. 1C). Glabrous and green, these nectaries are clearly visible against the golden brown pubescence of immature leaves, only beginning to unfold their leaflets (Fig. 1D), and apparently they remain functional throughout the life of the leaf. Both types of extrafloral nectaries, calyx and foliar, resemble one another in size, color and surface texture.

The encrustations of nectar collected from the extrafloral-calyx nectaries of three plants failed to dissolve completely. Although the results of these analyses are therefore of questionable validity, two are recorded here: (1) glucose 75.7, fructose 15.0, sucrose 9.3; (2) glucose 87.9, fructose 12.1, sucrose trace. The two samples of clear, viscous nectar from the extrafloral-calyx nectaries dissolved completely and contained the following proportions of sugars: (1) glucose 42.8, fructose 47.3, sucrose 9.9; (2) glucose 41.4, fructose 50.5, sucrose 8.1. The single sample of extrafloral-foliar nectar contained the following proportions of the three sugars analyzed: glucose 54.2, fructose 45.8, sucrose trace. Thus it appears from these limited data that the proportions of the three major nectar sugars are similar in both types of extrafloral nectaries; sucrose is low in comparison to both glucose and fructose. Although differences in proportions of glucose and fructose in extrafloral-calyx and -foliar nectar may exist, these data are insufficient to evaluate that possibility.

Floral nectar of two populations of *Erythrina flabelliformis* was also analyzed. The Molino Basin sample ($N = 7$) contained the following proportions of the three sugars: glucose $\bar{x} = 14.9 \pm 1.7$; fructose $\bar{x} = 22.1 \pm 1.4$; sucrose $\bar{x} = 62.9$

± 2.7. The Ráfagas sample (N = 10) contained the following: glucose $\bar{x}$ = 20.0 ± 2.7; fructose $\bar{x}$ = 21.3 ± 2.4; sucrose $\bar{x}$ = 58.7 ± 4.9. Sucrose is the dominant sugar in floral nectar and this contrasts with the situation in the two extrafloral nectars.

The nectars of *Erythrina flabelliformis* fall within two distinct types (dominant fructose and glucose; dominant sucrose) of three broadly classified types of angiosperm nectars identified by Percival (1961); the third type contains balanced amounts of sucrose, fructose, and glucose. Following comprehensive reviews of floral nectars, Wykes (1952b) and Percival (1961) concluded that the constituent sugars and their relative proportions tend to remain constant in a species, while their occurrence appears to be characteristic for certain families. Percival (1961) found long-tubed, leguminous flowers usually have sucrose dominant nectar. Baker & Baker (1980) confirm Percival's conclusions on within-family resemblances, but they note that the pollination biology of the species may influence the nectar type, even within taxonomic groupings.

Because of the possible presence of sucrose hydrolyzing enzymes, Bowden (1970) questioned the use of proportions of sucrose in nectars as a basis of classification, but Van Handel et al. (1972) felt that multiple sample consistency suggests the absence of the hydrolytic enzyme invertase, and they experimentally confirmed its absence in nectar of the century plant (*Agave sisalana*). Baker & Baker (1980) caution that in standing liquid nectar significant amounts of sucrose may break down due to natural nectar acidity or enzymes in the nectar (natural or introduced by micro-organisms). Quantitative variation in component sugars has been noted by Furgala et al. (1958) in the nectars of several legume crop plants and by Percival (1961) in 61 of 889 species studied. She (Percival, 1961) notes that although quantitative measurement may reveal that the nectar of all species varies within certain limits, these variations are not likely to alter their standing as to general nectar type.

Various authors have reported on the sugar constituents of extrafloral nectar (Percival, 1961; Baskin & Bliss, 1969; Bowden, 1970; Jeffrey et al., 1970; Butler et al., 1972; Elias et al., 1975; Keeler, 1977). A diversity of nectar types (sensu Percival, 1961) was found in various species, and both a correspondence and a lack of correspondence of nectar type was found between extrafloral and floral nectars of a species and between various extrafloral nectars, if present. Some plants have fructose-glucose dominant extrafloral nectar (Percival, 1961; Butler et al., 1972) as is reported here for *Erythrina flabelliformis*.

Percival (1961) reported associations between floral nectar type in some plants and the taxonomic group of the pollinators, but she noted that it is not known if differences in nectar composition (sugars) have any biological significance. Recently, Baker & Baker (1980) have argued that distinct types of nectar are characteristic of hummingbird-pollinated flowers (sucrose-rich), perching-bird-pollinated flowers (sucrose-poor), bat-pollinated flowers (sucrose-poor), nocturnal-moth-pollinated flowers (sucrose-rich), "true"-butterfly-pollinated flowers (sucrose-rich), and "bee-and-butterfly"-pollinated flowers (sucrose-poor). Baker & Baker (1975) have also noted correlations between several nonsugar constituents of nectar and classes of pollinators. Preferences for nectar type have

been investigated experimentally for two classes of flower visitors, honey bees (Wykes, 1952a; Waller, 1972) and hummingbirds (Hainsworth & Wolf, 1976; Stiles, 1976).

Evidence is accumulating which indicates that within the genus *Erythrina* species with sucrose-rich floral nectar are pollinated by hummingbirds and species with sucrose-poor floral nectar are pollinated by passerine birds (Cruden & Toledo, 1977; Baker & Baker, 1980, this symposium). Our results indicate that *E. flabelliformis* has floral nectar rich in sucrose. Thus, the proportions of sugars in the floral nectar of *E. flabelliformis* is in agreement with an apparent pattern found in the genus and amongst other hummingbird pollinated plants (Stiles, 1976; Cruden & Toledo, 1977; Baker & Baker, 1980).

The significance, if any, of differences in the proportions of the three dominant sugars in extrafloral and floral nectars of *Erythrina flabelliformis* is not apparent. Its understanding awaits definition of the roles and nectar preferences of associated fauna (hummingbirds, ants, nectar robbers, etc.), analysis of other nectar components, and/or other factors.

On June 11 five species of ants were noted visiting extrafloral-calyx nectaries of the 10 tagged plants at Ráfagas (numbers in parentheses indicate numbers of plants on which a species occurred): *Pseudomyrmex pallidus* F. Smith (1), *Crematogaster punctulata* Emery (8), *Forelius pruinosus* (Roger) (2), *Paratrechina* sp. (6), and *Camponotus ulcerosus* Wheeler (1). (Note: *Forelius pruinosus* has previously been in the genus *Iridomyrmex*.) Single plants harbored as many as three species. On June 4 and 18, 10 tagged plants at Molino Basin were also examined for ants visiting extrafloral-calyx nectaries. The five species encountered at Ráfagas were recorded here also (each species respectively on one, two, four, two and one plants) as well as two additional species, *Monomorium minimum* (Buckley) (1) and *Camponotus ocreatus* Emery (1). Two species of ants occurred on four plants; no ants were present on one of the plants; *Pseudomyrmex pallidus* were visiting corolla-damaged flowers on one plant. At Molino Basin on June 22 numerous *Crematogaster punctulata* were "robbing" floral nectar from an untagged plant.

The extended presence of *Crematogaster punctulata* at exposed floral nectaries of damaged flowers demonstrates acceptance of floral nectar by the ants, and suggests that factors other than ant-repellent characteristics of floral nectar chemistry (Janzen, 1977; Baker & Baker, 1978), such as morphological barriers in flower structure (Feinsinger & Swarm, 1978; Schubart & Anderson, 1978), are responsible for excluding some or all ants from floral nectaries of *Erythrina flabelliformis*.

Ants were observed at the extrafloral-foliar nectaries of eight of the tagged Molino Basin plants on August 5, 9, and 15. Five species of ants were seen visiting nectaries: *Pseudomyrmex pallidus* (3), *Monomorium minimum* (1), *Crematogaster punctulata* (4), *Forelius pruinosus* (3), and *Camponotus ulcerosus* (2).

Ants were seen visiting extrafloral nectaries on the calyces of floral buds during several stages of development: before the corolla appeared, while it was elongating and during anthesis (Fig. 1B). Throughout various periods of the

study ants were seen visiting foliar nectaries on juvenile leaves which had not unfurled their leaflets, and later, on fully developed leaves. Ants wandered over the inflorescences, stems, and/or leaves stopping briefly at the orifice of extrafloral nectaries (Figs. 1B, 1D), apparently to ingest small quantities of nectar, after which they would proceed to another extrafloral nectary. At Molino Basin, four of the five species of ants found on foliar nectaries had earlier been observed at calyx extrafloral nectaries of the same tagged plants. These observations suggest that on most plants the extrafloral nectaries, which are present from early in the initiation of flowering through leaf senescence, are visited by one or several species of ants throughout the flowering-leafing season.

The ecological role of ant visitation of extrafloral nectaries has received repeated attention over the years (Bequaert, 1922; Bailey, 1922; Wheeler, 1942; Bentley, 1977b). Recent studies in both tropical and temperate regions support the contention that a symbiotic, coevolved relationship exists between certain plants having extrafloral nectaries and the ants visiting them (Janzen, 1966, 1967; Hocking, 1975; Elias & Gelband, 1975; Bentley, 1976, 1977a; Tilman, 1978; Inouye & Taylor, 1979; Pickett & Clark, 1979). Feinsinger et al. (this symposium) recently reported that in three tropical species of *Erythrina* "inflorescences are protected by means of extrafloral [calyx] nectaries, which function to attract pugnacious ants."

Possibly one or more species of ants visiting extrafloral nectaries on *Erythrina flabelliformis* serve(s) a protective role in the ecology of the plant. If this proves to be the case, we speculate that the temporal phenological sequence of flowering season extrafloral-calyx glands followed by leafing period extrafloral-foliar glands may be adaptive for a seasonally extended myrmecophilous role.

The alkaloid-containing seeds of *Erythrina flabelliformis* (Hargreaves et al., 1974), although having a curarelike action (Folkers & Unna, 1939), suffer seed predation by larvae of a lepidopteran in Arizona (Raven, 1974; personal observations W.C.S.). Possibly, ants play a role in reducing seed predation by moth larvae. Such a seed-defense system in *E. flabelliformis* would combine (1) chemical deterrents incorporated within seeds with (2) seed-predator protection resulting from an ant-plant symbiosis fostered by extrafloral nectaries.

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EFFECTIVE POLLINATION OF *ERYTHRINA FUSCA* BY THE ORCHARD ORIOLE (*ICTERUS SPURIUS*): COEVOLVED BEHAVIORAL MANIPULATION?[1]

EUGENE S. MORTON[2]

ABSTRACT

Based on observations in Panama, the male orchard oriole is shown to be the most effective pollinator of *Erythrina fusca*. It is hypothesized that the identical color of the male oriole's body plumage and the floral parts surrounding the nectar indicates a coevolved relationship.

Erythrina fusca Loureiro is a large and abundant tree in the Panama Canal Zone and occurs pantropically (Krukoff & Barneby, 1974). I observed nectar-feeding birds visiting a pure stand of *E. fusca* growing in swampy ground near the Pedro Miguel locks of the canal (Table 1). The avian activity in 4 tree crowns was observed for a total of 16 hours during January and March 1974 and March 1975. The orchard oriole (*Icterus spurius*) vastly outnumbered all other species combined both in numbers present and in total time spent nectar-feeding. This species's outstanding importance to the effective pollination of *Erythrina fusca* here is underlined by four facts that form the basis for the hypothesis that *E. fusca* and this oriole may have coevolved.

1. Of the 13 bird species observed feeding on *Erythrina fusca* nectar, only the male orchard oriole correctly opened the flowers (see below) to obtain nectar and to receive pollen for transfer to other flowers. The others either robbed nectar by piercing the calyx or standard base, by using only extrafloral nectaries, or by visiting only flowers previously opened by the orchard oriole.

2. The orchard oriole, a migrant that breeds in North America, occurs in large flocks of up to several hundred, far exceeding the numbers of other potential avian pollinators. This species robs nectar from other species of trees, such as *Tabebuia guayacan* (Seem.) Hemsley, easily piercing the corolla with its long sharp bill, but not from *Erythrina fusca* flowers.

3. Only adult male orchard orioles were observed to open *Erythrina fusca* flowers. Females and immature males, which have greenish olive plumage, were excluded by the black and burnt orange adult males. The burnt orange color of the adult male oriole is exactly matched by a portion of the *E. fusca* flower that becomes visible only after the standard has been pushed back.

4. *Erythrina fusca* flowers during a period when the orchard oriole is most abundant.

These facts will be discussed together with corollary information on the bird and the plant to support the hypothesis that the plant is manipulating the behavior of the male oriole to most effectively affect pollination, particularly outcrossing.

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Phenology of *Erythrina fusca*

Erythrina fusca begins to show mature inflorescences nearly synchronously on both Pacific and Atlantic slopes of the Canal Zone at the beginning of the dry season. On 29 December 1974, trees at both the Pedro Miguel locks site, which is about 10 km from the Pacific coast, and trees near Gatun, 4 km from the Atlantic coast, had an estimated 1% mature flowers. Flowering lasted from then until 4 March 1975 (66 days), when the smaller trees still had unopened flowers. Figure 1 shows the manner in which flowers are arranged. The flowers are arranged radially around the thick stem which provides a strong perch for the oriole. There are from 2 to 12 inflorescences in each cluster, a flower measureing about 50 mm from the calyx to the tip of the standard.

Leaves are shed before flowers mature as is typical for many *Erythrina* (Standley, 1922). The flowers are highly visible and appear uniform dull yellow-orange until opened when the rich burnt-orange color of the wing petals is uncovered.

Shortly after the flowering period ends, leaves appear coincident with the onset of the rains in late April. The next season's flower buds form at this time but remain in an immature stage throughout the rainy season. The calyx attains a mature size early and its tough texture no doubt protects the immature parts within. Significantly, an extrafloral nectary located at the tip of the calyx (see Fig. 1), secretes nectar during this 8 to 9 month period between bud formation and flower maturation. Probably these nectaries function to nourish ants (species undetermined) which live in the tree's hollow twigs (pers. obs.; see also Feinsinger et al., this symposium). However, several bird species were observed to use this extrafloral nectar source (Table 1). Some pods attained mature size even while flowers were maturing, but they dried and opened when flowering stopped in the late dry season (April).

Orchard Oriole Behavior

general behavior

This oriole, wintering from southern Mexico to southern and central eastern Colombia and northwestern Venezuela (Anonymous, 1957), becomes abundant in Panama during late September and remains in large numbers until late March. During fall their center of abundance is the drier Pacific slope where they concentrate on the flowers of trees such as *Luehea* sp. Large night roosts of several thousand birds form from the congregation of smaller flocks streaming in from all directions. With the advent of the dry season orchard orioles begin foraging for nectar in synchronously flowering trees such as *Tabebuia* sp. and then *Erythrina fusca*. Orchard oriole flocks nectar-feeding in all species of trees *except Erythrina fusca* are composed of all sex and age classes; only adult males (rarely first year males) are found in *E. fusca* trees. This observation is so common among ornithologists familiar with the species that it is mentioned in a field guide to bird identification (Ridgely, 1976)! This is not due to choice on the female's part. The females are largely excluded because adult males are

TABLE 1. Species of birds and their characteristics while nectar-feeding on *Erythrina fusca*.

Species	Floral Parts Searched[a]	Ave. Peak Numbers/Tree
Orange-chinned parakeet (*Brotogeris jugularis*)	NR, eats pollen too	6
White-necked jacobin (*Florisuga mellivora*)	FAO	1
Rufous-tailed hummingbird (*Amazilia tzacatl*)	FAO	1
Red-crowned woodpecker (*Melanerpes rubricapillus*)	NR, FAO	2
Red-legged honeycreeper (*Cyanerpes cyaneus*)	FAO, EFN	10
Tennessee warbler (*Vermivora peregrina*)	FAO, EFN	5
Yellow-backed oriole (*Icterus chrysater*)	FAO, NR	3
Orchard oriole (*Icterus spurius*)	OF, FAO	128
Northern oriole (*Icterus galbula*)	FAO	5
Blue-gray tanager (*Thraupis episcopus*)	FAO, NR, EFN	4
Palm tanager (*Thraupis palmarum*)	NR, FAO	4
Crimson-backed tanager (*Rhamphocelus dimidiatus*)	NR, FAO	6
Streaked saltator (*Saltator albicollis*)	NR	2

[a] Abbreviations. FAO = flowers already opened; NR = nectar robber; OF = open flowers; EFN = extra-floral nectary.

able to dominate them in aggressive encounters. It is possible that females can locate *E. fusca* trees without aggressive males and obtain nectar from them.

ORCHARD ORIOLE BEHAVIOR WHILE IN *ERYTHRINA FUSCA* TREES

Aggressive Behavior.—The occurrence of birds in flowering *Erythrina fusca* trees is dynamic. At one moment there are no birds in the crown, the next moment the crown is filled with 30 or more orchard oriole males chasing each other, females, and the smaller honeycreepers while continuously uttering a harsh aggressive chatter. After the initial sorting out of feeding positions the chattering subsides but is resumed whenever a straggler flies into the tree. It is impossible to document the amount and direction of aggressive chases and displacements by the inhabitants of an entire tree crown so I watched three orchard oriole males from 1200 to 1300 hrs that were typical of the rest. Each averaged 9 chases directed against other male orchard orioles, 12 against female and immature male

orchard orioles, 20 chases against red-legged honeycreepers (*Cyanerpes cyaneus*), one against a Tennessee warbler (*Vermivora peregrina*). With each male oriole chasing about once each 1.4 minutes a tree with 30–40 males presents an active scene.

Both male and female northern orioles (*Icterus galbula*), a less common migrant, fed upon already opened *Erythrina fusca* flowers and were dominant over orchard orioles. The red-crowned woodpecker (*Melanerpes rubricapillus*) occurred as a single pair within one tree crown, each pair excluding other woodpeckers, and displacing orchard orioles infrequently but at will. Orchard orioles ignored and were ignored by the similarly sized palm and blue-gray tanagers (*Thraupis palmarum* and *T. episcopus*). I also saw no interaction between orchard and the three resident yellow-backed orioles (*Icterus chrysater*), but the resident orioles did chase off conspecifics once. Orange-chinned parakeets (*Brotogeris jugularis*) occasionally chased conspecifics, but they were ignored by the other bird species. Crimson-backed tanagers (*Ramphocelus dimidiatus*) were also ignored by orchard orioles.

Orchard orioles exhibit a lower "social tolerance" in the presence of *Erythrina fusca* nectar than when feeding on other tree nectars. This is likely due to the relatively rich nectar source provided by *E. fusca* (see below). Social tolerance is often a highly flexible aspect of avian behavior and is known to be influenced by the economics of food exploitation strategies (Leck, 1972). The high caloric content of nectar also permits, in a proximal sense, the high rate of costly high energy chases that permit access to nectar. As an ultimate factor, nectar feeding reduces the need for effort expended hunting insects that are high in protein but low in calories (Ford & Paton, 1976).

Nectar-Feeding Behavior.—The time orchard orioles remain in their defended area in an *Erythrina fusca* crown is important to the coevolutionary hypothesis. During the 16 observation hours the orioles were actively opening flowers for only about 5 hours. Most of the time was spent off the *E. fusca* trees in trees retaining their leaves. Here these were predominantly *Guazuma ulmifolia* Lam. Male and female orioles were in flocks and showed little aggression. Some insect foraging was observed, primarily by females, but preening and "loafing" occupied most time. A few males could be found in *E. fusca* crowns during lulls in nectar feeding, but the vast majority alternated between rushing into the *E. fusca en masse*, spending 20–30 minutes nectar feeding then retiring to densely leaved trees for insect foraging and resting. No individual birds were banded so it is not known if a male returns to the same place in an *E. fusca* crown. The observations suggest that a tree crown is a "grab bag" and that individual birds do not retain the same foraging dominance area every time they return to the trees.

As shown in Table 1, the male orchard oriole was the only bird to correctly open the *Erythrina fusca* flowers. *Erythrina fusca* flowers are erect on the parent rachis even though radially arranged on it (Fig. 1). The commissure formed by the lateral margins of the standard faces inward towards the rachis such that a bird approaching the flowers along the rachis would confront the commissure. The rhombic-ovate blade of the standard completely encloses the other floral

parts in the unopened mature flower. To obtain nectar, the orchard oriole sidles down the rachis, places its bill into the commissure while facing downward, opens the bill when it is fully inserted[3] and at the same time pushes with its head. In a mature flower this will cause the standard to fall backwards, its constricted base acting as a hinge. When this happens, the stamens and style are released against the bird's throat and upper breast. This action by the bird seems to take some effort and some, probably immature flowers, are not opened even though probed. It is doubtful that even the largest bees (e.g., *Eulaema* sp.) can gain access to the nectar. An opened flower contains such quantities of nectar that an oriole will sip from four or five flowers and quit.

Except for the orchard oriole, other species robbed the flowers by clinging to the rachis from beneath and puncturing the standard or calyx (Fig. 1), or they visited flowers already opened by the oriole. They did not align themselves in any consistent manner to receive pollen and probably contribute relatively little to the pollination of *Erythrina fusca* in Panama.

Nectar Constituents.—Herbert and Irene Baker kindly sent an analysis of a nectar sample taken from the trees I observed (Table 2). The histidine scale score of 7, an index to amino acid concentrations, is extremely high for a bird-pollinated flower (ave. of 21 species was 3.31) (Baker & Baker, 1975). This concentration might diminish the need for insect food for male orchard orioles relative to females. This would concur with the observation that females, excluded from *Erythrina fusca* trees, spend more time insect hunting than males when *E. fusca* nectar is available.

Discussion

The data presented show that the orchard oriole is the most effective pollinator of *Erythrina fusca* flowers among the bird species observed. But it is the color of the floral parts surrounding the nectar, identical to the male oriole's body plumage, that indicates a coevolved relationship. I suggest that this color is both attention-getting and aversive to a male orchard oriole. Furthermore, it only shows in a flower that has been opened and drained of nectar. Thus the more flowers an oriole has opened in the small foraging area to which the bird is restricted because of the aggressive conspecifics surrounding it, the more "signals"

[3] Of the birds visiting *E. fusca*, only orioles use this bill scissoring technique in foraging. They often hunt insects in dead twig tips by inserting the bill, opening it, and then looking down the open bill commissure for exposed prey. This may have preadapted them for correctly opening *E. fusca* flowers.

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Figure 1. In the foreground, a male orchard oriole (*Icterus spurius*) is about to open a flower of *Erythrina fusca*. The two opened flowers at the rachis tip show the bright oriole-matching color of the wing petal tips. In the center, a rachis with immature flowers shows the prominent extrafloral nectary located on the calyx tip. In the background, a palm tanager (*Thraupis palmarum*) is shown in the hanging position taken by several nectar-robbing species as they prepare to pierce the calyx or standard from below.

TABLE 2. Nectar constituents from *Erythrina fusca* in Panama.

Reagents	Results
Ninhydrin	7 on histidine scale = 3.125 μmols/ml
Osmic acid	No saturated lipids
Dichlorophenol-indophenol	Some organic acids
Dragendorff's	No alkaloids
p-Nitraniline	No phenols
Brom-phenol Blue	No proteins

Amino-acid Analysis

Alanine	++	Methionine	+
Arginine	+	Phenylalanine	+−
Glutamic	+−	Proline	++
Glycine	+	Serine	+−
Histidine	+	Threonine + Glutamine	++
Isoleucine	+	Tyrosine	+−
Leucine	+	Valine	+
Lysine	+	plus two non-protein amino acids	

Sugar concentration of 20% (w/w) sucrose equivalents; fructose 30%, glucose 42%, sucrose 28%. Ratio of sucrose to glucose plus fructose = 0.40.

it receives to move on to another tree. The value to the *E. fusca* tree in incorporating the oriole's color in this manner is therefore to increase outcrossing. In addition to the color, the rhombic-ovate blade of the standard is designed to conceal this color until it is needed to, in essence, repel the oriole, i.e., after the individual is covered with pollen to be carried elsewhere.

Obviously, this is only a hypothesis, but one that has an inherent test yet to be made. If there is a coevolved relationship between orchard oriole and *Erythrina fusca* in Panama, then one would predict that *E. fusca* populations should have different flower coloration where the orchard oriole does not occur. Snow & Snow (1972) list the color of *E. glauca* (= *fusca*) in Trinidad as red. However, Feinsinger (pers. comm.) reports the flower color the same as the Panamanian population. From a color slide sent to me by Feinsinger, it appears that the Trinidadian flowers do differ: the calyx is wine or reddish color in flowers from Trinidad, dull brown in Panama. The wing petals and standard look the same from both areas. Trinidad is the same latitude as my study site (9° N) but orchard orioles do not occur on Trinidad (Ffrench, 1973). The question remains if flowers still more remote from the wintering range of orchard orioles will lose the burnt orange color. In Malaya, the color is "purple" (Corner, 1940).

Since the orchard oriole is confined in winter primarily to Middle America and *Erythrina fusca* occurs pantropically, the opportunity exists for a comparative study of pollinator–*E. fusca* coevolution. Does species-specific coevolution involve a threshold in pollinator abundance with some *E. fusca* floral parts assuming the generalist bird attracting color of red in regions where an abundant migrant species is not found?

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PASSERINE POLLINATION OF *ERYTHRINA MEGISTOPHYLLA* DIELS (FABACEAE)[1]

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ABSTRACT

Floral morphology and behavior, nectar composition and observational data suggest that *Erythrina megistophylla* is adapted to passerine bird pollination. It has short, open-mouthed, backwardly directed flowers on horizontal racemes. The primary visitors are members of the Coerebidae (honeycreepers), passerine birds which perch on the inflorescence rachis while probing the flowers. The nectar has a low sugar concentration (6–9% W/V), is hexose dominant, and contains a high concentration of amino acids.

Pollination of Old World *Erythrina* species by perching birds (Passeriformes) has been known for some time (Ali, 1932; Docters van Leeuwen, 1932; Porsch, 1924; Singh, 1929), although similar pollination of species of this genus in the New World has gone largely unnoticed, probably due to the vast majority of hummingbird-pollinated species. Fifty-two of the 64 New World species of *Erythrina* are adapted to hummingbird pollination (as presented by Toledo, 1974). This estimate is based on descriptions and illustrations provided in Krukoff & Barneby's (1974) treatment of the genus. This leaves 12 species which show adaptations to "perching" or passerine birds.

Observations have been made on visitations to some of these species by several authors (Leck, 1974; Raven, 1974; Skutch, 1954; Snow & Snow, 1971; Steiner, unpubl.; Timken, 1970). Cruden & Toledo (1977) and in this symposium Feinsinger et al., Morton, and Toledo & Hernández have considered the syndrome for New World species of *Erythrina* in detail. Their studies have helped demonstrate that in the New World a "perching bird" syndrome based on floral morphology and nectar composition definitely exists. The nectar of *Erythrina breviflora* A. DC. studied by Cruden & Toledo (1977) differed from that of a typical hummingbird *Erythrina* (*E. coralloides* A. DC.) on the basis of sugar concentration, ratio of the sugars (glucose and fructose/sucrose), and on the concentration of amino acids. The analysis done by Irene Baker showed that *E. breviflora* had hexose-dominated nectar that was less concentrated and contained a greater proportion of amino acids than the sucrose rich nectar of the hummingbird adapted *E. coralloides*.

Since *Erythrina breviflora* is considered by Krukoff & Barneby (1974) to be phylogenetically primitive, the perching bird syndrome is most probably a primitive condition that has been retained by some New World species. Perhaps the most important adaptive change that has occurred facilitating hummingbird pollination among *Erythrina* species has been the morphological switch from

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short, open-mouthed corollas directed inwardly to long closed corollas directed outwardly. The more primitive short corollas are borne in horizontal racemes whereas the more specialized long corollas are borne in vertical racemes. Clearly, one permits perched probing for nectar while the latter makes hovering in mid-air necessary. These morphological changes reduced the number of birds that could successfully obtain nectar and therefore cut down on unspecialized opportunistic feeders that may have been less efficient pollinators than hummingbirds.

In addition to the obvious morphological changes, there has been a change in nectar composition associated with the transition from perching-bird- to hummingbird-pollinated *Erythrina* species. The nectar of perching-bird-pollinated *Erythrina* species may have less concentrated, hexose-dominated nectar with significantly more amino acids (Cruden & Toledo, 1977; Baker & Baker, 1980; Baker & Baker, this symposium). Thus, visitation and nectar data were collected for *Erythrina megistophylla*, a species morphologically similar to *Erythrina breviflora*, in order to provide further evidence for the existence of a passerine bird pollination syndrome in the New World.

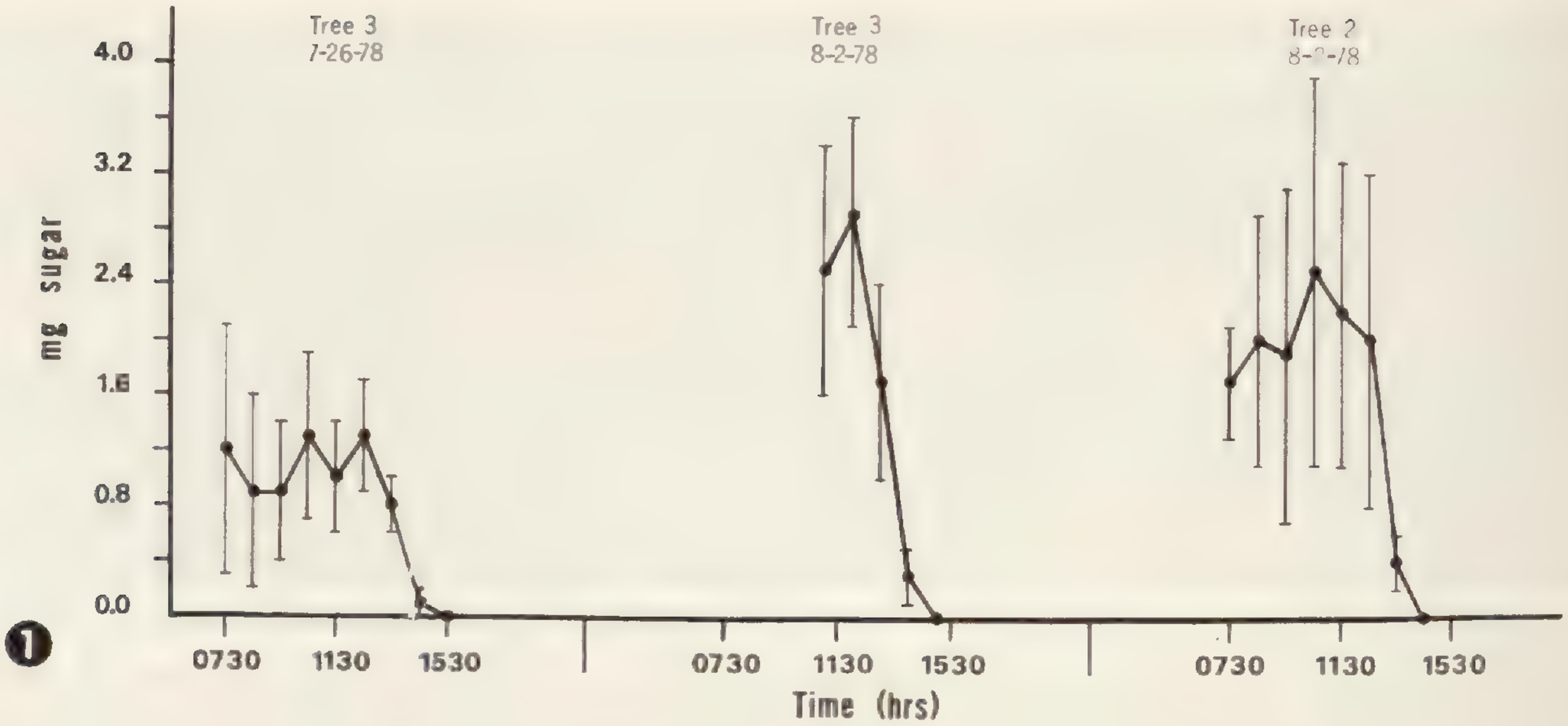
Study Site and Methods

This study was carried out at the Río Palenque Science Center located 65 km south of the equator, between Santo Domingo and Quevedo in the Pacific lowlands of central Ecuador (see Dodson & Gentry, 1978, for further details). Field observations and measurements were made on *Erythrina megistophylla* during two periods between 20 July 1978 and 2 Aug. 1978. *Erythrina megistophylla* is an understory tree of up to 4 m and is a fairly common component of disturbed and mature portions of the wet forest (sensu Holdridge) at the Science Center (Dodson & Gentry, 1978). In addition to its characteristic floral morphology, it is distinguished by the presence of a single-seeded, baseball-sized fruit and very large (ca. 30 cm) leaflets.

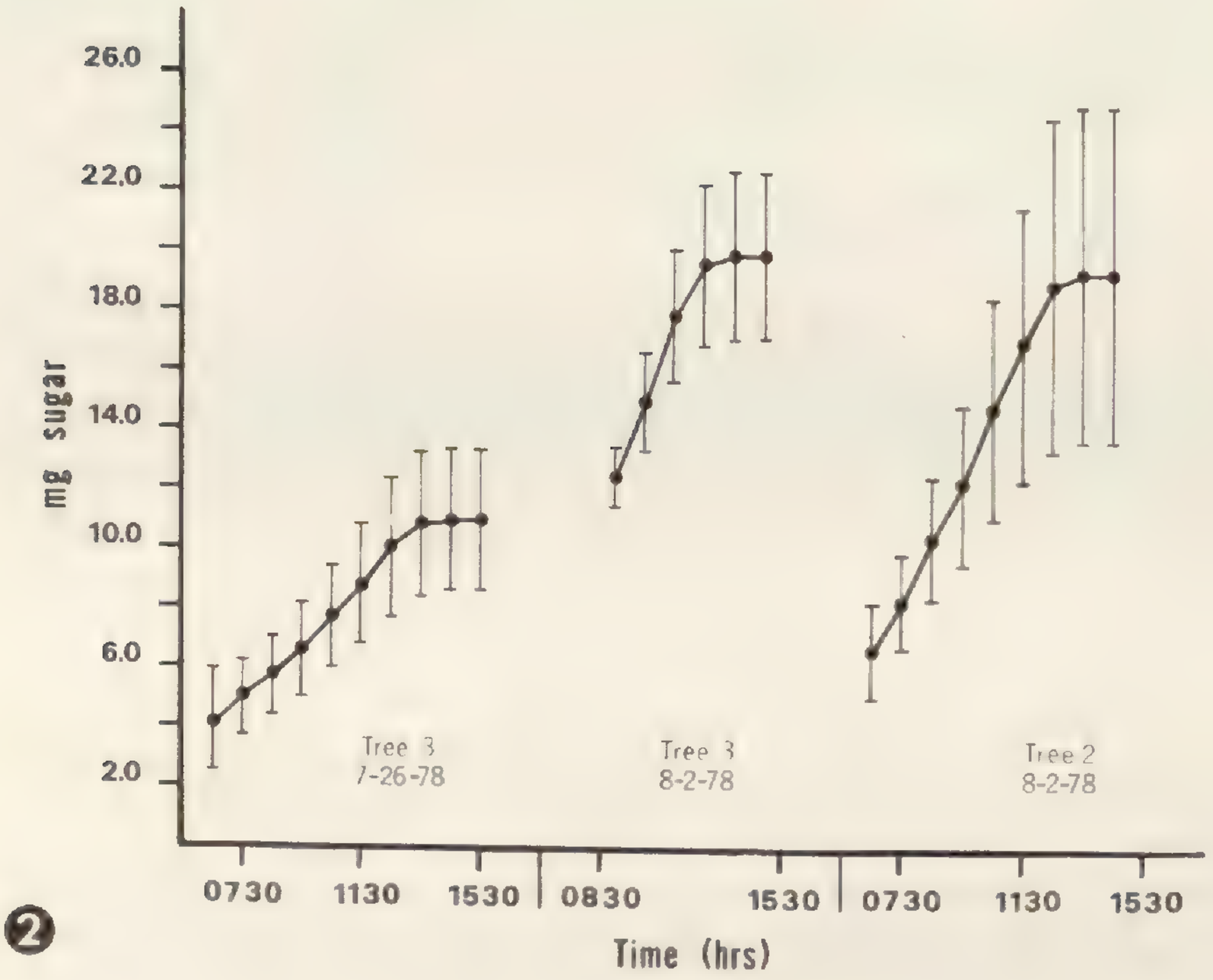
During each period of observation, floral visitors and nectar secretion patterns were recorded for *Erythrina* individuals. Observations totaling 60 hours from 0600 to 1700 EST were made on 4 trees at the Science Center. Three of these were located in forest edge habitats while the fourth was in the forest.

Two different trees on two different days (one week apart) were utilized for continuous nectar sampling (see Figs. 1–3). The same inflorescences on each tree were sampled both times. Data from tree 3 are an average of 10 flowers from two inflorescences, while only 5 flowers from a single inflorescence were measured for tree 2. Continuous nectar sampling consisted of hourly samples beginning at 0630 EST and ending when nectar secretion ceased (which was usually between 1350 and 1550) (Fig. 1). Five individual flowers were numbered on each inflorescence enabling the pattern of secretion for each flower to be followed. Nectar was easily removed repeatedly without injury to the flowers. Except when taking measurements, inflorescences were covered with nylon mesh bags, beginning prior to anthesis, to eliminate nectar removal by visitors during the sampling period.

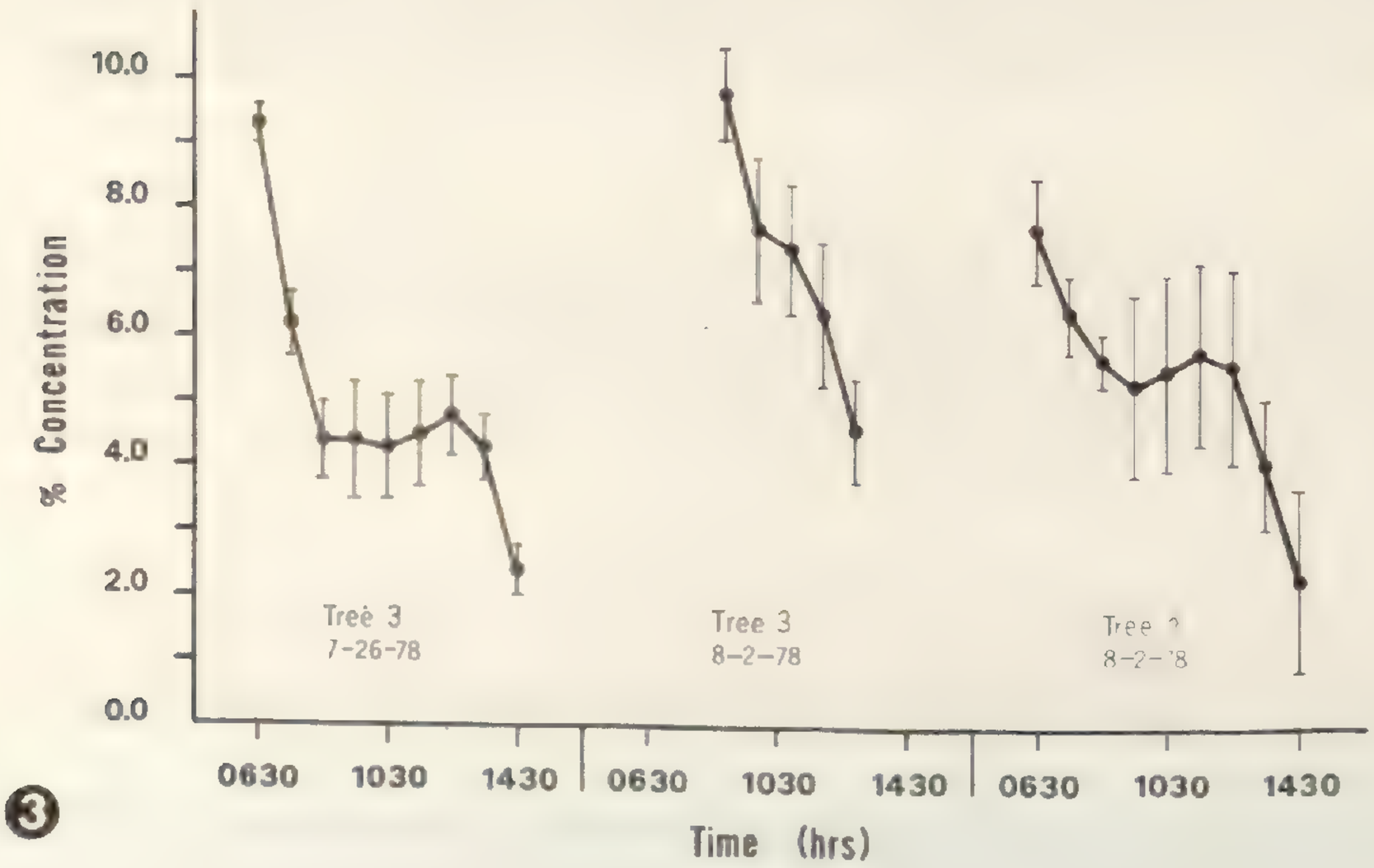
Volume measurements were obtained using calibrated micropipets. Nectar


Tree 3
1-26-78
Tree 3
8-2-78
Tree 2
8-2-78
mg sugar
4.0
3.2
2.4
1.6
0.8
0.0
0730
1130
1530
0730
1130
1530
0730
1130
1530
Time (hrs)

1


mg sugar
26.0
22.0
18.0
14.0
10.0
6.0
2.0
Tree 3
1-26-78
Tree 3
8-2-78
Tree 2
8-2-78
0730
1130
1530
0830
1530
0730
1130
1530
Time (hrs)

2


% Concentration
10.0
8.0
6.0
4.0
2.0
0.0
Tree 3
1-26-78
Tree 3
8-2-78
0630
1030
1430
0630
1030
1430
0630
1030
1430
Time (hrs)

3

concentration was measured for each sample. This was done by using a pocket refractometer that allowed correction of readings to a standard temperature of 23°C. The refractometer measurements which are weight/total weight percentages were converted to weight/volume percentages so that nectar production could easily be expressed as mg equivalents of sugar (volume × concentration × density of sugar). Nectar analysis was done by Irene Baker (see Baker & Baker, 1976 for methodology).

In order to determine whether continuous nectar removal affected total nectar production and concentration, inflorescences were bagged as before and flowers sampled once at the end of the day. Both volume and concentration of nectar were measured.

Results

Floral behavior

Erythrina megistophylla had an average of 9.4 inflorescences per tree (S.D. = 2.1, n = 5) during the study period. An inflorescence produced an average of 5.2 ± 1.4 (n = 18) new flowers per day. Based on this and the number of pedicel scars and buds present on sampled inflorescences, an inflorescence might produce flowers from at least 40 to more than 70 days. Since flowering times of the inflorescences are not synchronized, a single tree could potentially flower for several months. Although no information is available on the duration of flowering for this species at Río Palenque, like *E. breviflora* of Mexico (Cruden & Toledo, 1977), it probably flowers for several months.

Fruit set on individuals examined appeared rather low considering the large number of flowers produced. The average number of mature fruits produced was about one per inflorescence; however, this may be an underestimate since some inflorescences had many flower buds (therefore potential fruit) at the time of this study. It is not possible from fruit crop estimates to know how many flowers were actually pollinated since due to the size of mature fruits, it is likely that space and energetic constraints limit total fruit production. Figure 5 shows a clump of ca. seven very young fruits close together. It is doubtful that all of these fruits could mature along such a short portion of the rachis.

Nectar secretion

The flowers of *Erythrina megistophylla* opened, with nectar present, between 0515 and 0615 EST and lasted for a single day. They were abscised daily whether visited or not. Figure 1 compares the rate of nectar secretion while Fig. 2 presents the average cumulative nectar production of a flower for two different trees. Tree 2 was sampled on two different days. It is apparent from these graphs that nectar production variability between flowers was very high. Clearly, for the

←

Figures 1–3. Characteristics of nectar from flowers of *Erythrina megistophylla*.—1. Average rate of sugar production of an individual flower.—2. Average cumulative sugar production of an individual flower.—3. Average nectar concentration (W/V) of an individual flower.

same tree there is a daily component to this variability. Samples from tree 2 and tree 3 on 2 Aug. 1978 were much more similar than comparisons for tree 3 when sampled on different dates. The higher rate and overall production on 2 Aug. 1978 as compared to 26 July 1978 may be explained by a difference in weather conditions. On 2 Aug., it was clear and hot, while on 26 July it was overcast and warm. Both solar radiation and temperature have been shown to influence nectar production (Shuel, 1955; Beutler et al., 1957). The nectar present at anthesis was removed at 0630, thus subsequent hourly measurements represent the amount of nectar secreted during the previous hour.

Figure 3 illustrates how average nectar concentration of a single flower changed during the secretion period. It is evident when comparing this Fig. 3 with Fig. 1 that variability in sugar secretion results primarily from changes in the volume secreted, rather than in the sugar percentage. Tree 3 (2 Aug. 1978) had a slightly different curve since sampling was initiated later in the morning.

Although Raw (1953) found that nectar removal for flowers of *Rubus* species stimulated nectar production, data presented in Tables 1 and 2 provide no evidence that nectar removal stimulates nectar production in *Erythrina megistophylla*. Values indicated by *b* in Table 1 represent averages of the total nectar produced (summed hourly samples) over the secretion period. The other values are averages for flowers in which nectar was removed only at the end of the secretion period.

An inflorescence from tree 3 on 21 July 1978 produced an average of 12.6 ± 2.6 mg sugar per flower for a single end of day sample. On 26 July 1978 and 2 Aug. 1978 it was sampled hourly and produced total averages of 11.5 ± 2.8 and 19.8 ± 2.8 mg sugar, respectively. Thus the daily variability in total nectar secreted prevents one from making any definite conclusions about the effects of nectar removal. A similar situation occurred for tree 2 where variation between totals for end of day nectar sampling was greater than variation between hourly and end of day sampling.

Table 2 presents the average nectar concentration of a flower (weight/volume of solution) for single and multiple samples. These data suggest that the slight differences found in Table 1 are a reflection of changes in concentration of the nectar secreted.

NECTAR ANALYSIS

The nectar of *Erythrina megistophylla* is similar in composition to that of *E. breviflora* (Baker, I., pers. comm.). It is clearly hexose dominant (sucrose/glucose + fructose of less than 0.015) with a sugar concentration of less than 10% (see Table 2) and contains a high concentration of amino acids (ca. 3.9 mg/ml). It also contains a large number (20) of different amino acids, as do *E. breviflora* and *E. fusca* Loureiro, with 18 and 17, respectively (Cruden & Toledo, 1977). Hummingbird *Erythrina* species (*E. coralloides* and *E. herbacea* L.), in contrast, have been found to contain fewer and less concentrated amino acids with greater proportions of sucrose (sucrose/glucose + fructose of 0.47 and 0.668, respectively; Cruden & Toledo, 1977; Baker & Baker, this symposium).

TABLE 1. Average total nectar production (mg sugar) of a flower of *Erythrina megistophylla.*

Tree	21 July 1978	26 July 1978	2 Aug. 1978
1	15.4 ± 1.8[a]	22.8 ± 1.1	—
2	23.3 ± 2.3	28.5 ± 0.5	19.2 ± 5.6[b]
3	12.6 ± 2.6	11.5 ± 2.8[b]	19.8 ± 2.8[b]
5	32.9 ± 5.9	—	—
7	—	36.8 ± 2.5	—

[a] Standard deviation.
[b] Average of total nectar removed (summed from hourly samples).

FLORAL VISITORS

A list of the bird visitors to *Erythrina megistophylla* is presented in Table 3. Since many of these visitors were seen at only one or two of the study trees, an importance value was calculated based on the number of foraging visits and proportion of study trees visited. This gives a better estimate of the importance of any particular visitor at the Río Palenque site as a whole.

A comparison of importance values indicates that the male green honeycreeper was the most important visitor to *Erythrina megistophylla* during the study period (see Fig. 5). It was the only species that regularly visited all of the study trees throughout the observation period. It remains unknown, however, whether or not the male green honeycreeper is a regular visitor over the entire period of flowering and since birds were not marked, it is difficult to accurately assess their degree of individual constancy.

While the bananaquit also had a high importance value, it was not seen regularly at all trees throughout the study. It was seen at three of the study trees, but only on 1 Aug. and 2 Aug. On one occasion a bananaquit was seen flying from *Erythrina megistophylla* to a *Heliconia* species. Snow & Snow (1971) observed bananaquits in Trinidad at 50 different flowering species, indicating they are able to exploit a wide range of flowers for nectar. This suggests that shifts in the pollinator community may take place during the flowering period of the tree. Since it flowers for several months, it is likely that at various times some *Erythrina* visitors may be drawn away by more productive resources.

TABLE 2. Average nectar sugar concentration (% W/V) of a flower of *Erythrina megistophylla.*

Tree	21 July 1978	26 July 1978	2 Aug. 1978
1	6.7 ± 0.4[a]	8.2 ± 0.8	—
2	7.7 ± 0.5	8.3 ± 0.2	6.5 ± 0.3[b]
3	6.3 ± 0.8	6.5 ± 0.3[b]	8.9 ± 0.6[b]
5	8.7 ± 0.4	—	—
7	—	10.1 ± 0.3	—

[a] Standard deviation.
[b] Average concentration (summed from hourly samples).

TABLE 3. Visitation frequency, number of trees visited, and importance of the bird visitors to *Erythrina megistophylla*.

Family and Scientific Name	Common Name	Total Foraging Visits (1)	Proportion of Study Trees Visited (2)	Importance (1 × 2)
Coerebidae	Honeycreepers			
Chlorophanes spiza	Green honeycreeper	58	1.0	58.0
Coerba flaveola	Bananaquit	28	0.75	21.0
Dacnis lineata—male	Black-faced dacnis	2	0.25	0.5
—female		18	0.25	4.5
Thraupidae	Tanagers			
Ramphocelus icteronotus—male	Yellow-rumped tanager	10	0.75	7.5
—female		8	0.75	6.0
Mitrospingus cassinii	Dusky-faced tanager	2	0.50	1.0
Euphonia saturata	Orange-crowned euphonia	5	0.25	1.25
Trochidilidae	Hummingbirds			
Amazila tzactl	Rufous-tailed hummingbird	5	0.25	1.25
Thalurania colombica—male	Crowned woodnymph	41	0.25	10.25
Unidentified individuals	----------	23	0.75	17.50
Unidentified	----------	2	0.50	1.0

FIGURES 4–5. Birds visiting flowers of *Erythrina megistophylla*.—4. Bananaquit.—5. Male green honeycreeper.

Figures 4 and 5, respectively, show a bananaquit and a male green honeycreeper visiting the flowers of *Erythrina megistophylla.*

Other visitors with fairly high importance values include the male crowned woodnymph, male and female yellow-rumped tanagers and the female black-faced dacnis. Both the crowned woodnymph and the black-faced dacnis, despite being frequent visitors, were each seen at only one of the four study trees. This would suggest that they are probably less effective pollen dispersers than honeycreepers and bananaquits.

The large number of foraging visits by the male crowned woodnymph occurred at a single *Erythrina* individual located in the forest. Many of these visits were in conjunction with territorial defense against other birds including bananaquits, orange-crowned euphonias, and some unidentified hummingbirds. After chasing an intruder away, the crowned woodnymph would visit a few flowers and then return to its perch.

The unidentified hummingbird category had the third highest visitor importance value (Table 3). It is unfortunately impossible to know how many different species this represents. Seventy-four percent of these visits were to the tree visited by the crowned woodnymph. This suggests that frequent hummingbird visitation may occur in some situations; however, additional observations are needed to determine the extent of such visitations.

The primary interest of the orange-crowned euphonias was the fruit of *Lysianthus synanthera* (Schlecht.) Bitt. (Solanaceae), which was within 1–2 m of the *Erythrina* tree. Their visits to *Erythrina* occurred along with fruit eating at *Lysianthus* and may have been purely opportunistic as they did not regularly visit *Erythrina* flowers. It became obvious that these birds were more interested in fruit than nectar, since numerous return visits were made to *Lysianthus* without corresponding visits to *E. megistophylla.* During one visit, a *Euphonia* was quite destructive to flowers by removing stamens as it probed them. This provides additional evidence that euphonias are not important pollinators of *Erythrina megistophylla.*

Figure 6 presents daily visitation patterns of the six most important visitors to *Erythrina megistophylla.* The male green honeycreeper was the most regular visitor throughout the day. All birds, except the crowned woodnymph and the male yellow-rumped tanager visited most frequently between 0800 and 1000 EST. These two birds had visitation peaks at 1330 and 1400 EST, respectively. The earliest visit made by any bird was between 0630 and 0700 EST, while no visits were recorded later than 1430 EST. This pattern corresponds nicely with the nectar secretion pattern. No nectar was secreted in any flowers after 1430 EST (see Fig. 1).

Since two of the *Erythrina* individuals observed were within 50 m of each other, they could be watched simultaneously in order to follow movements of individuals. Of the birds that frequented these two trees, both the green honeycreeper and the yellow-rumped tanagers flew between them regularly. These birds, therefore, are actively searching for *Erythrina* flowers and thus are potentially effective cross-pollinators.

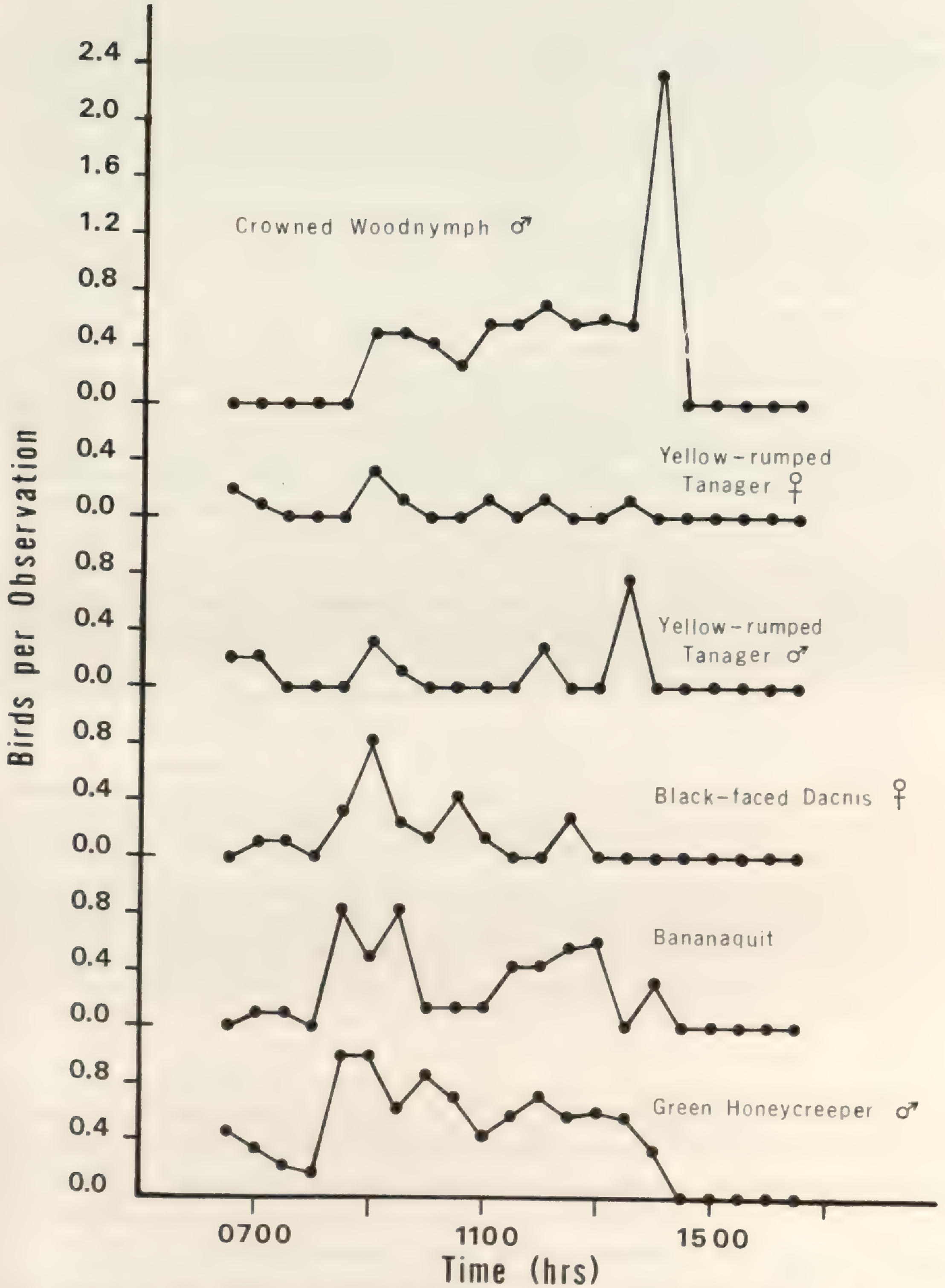


FIGURE 6. Daily visitation patterns of the six most important bird visitors to flowers of *Erythrina megistophylla*.

DISCUSSION

An interesting point brought out by the continuous nectar sampling data is that nectar concentration changes over the secretion period. It can be seen from Fig. 3 that there is an initial drop at the beginning of the secretion period to a fairly constant level which lasts until 1–2 hours before the cessation of nectar flow. It is important to recognize that nectar concentration, as well as volume, changes during the period of nectar secretion. Both factors, then, influence the amount of sugar available to floral visitors. Only through continuous nectar sampling can one get a realistic picture of the food availability at any given time of day.

By examining the cumulative nectar secretion pattern of an average flower (Fig. 2), it becomes clear that the first visitor to the tree in the morning has access to more sugar per flower than at any other time of day. If *Erythrina megistophylla* nectar comprises a significant proportion of the daily food supply for its bird visitors, one might expect selection for earlier visitation. Without knowing more about the habits of these birds at this particular site, however, it is difficult to evaluate constraints which may prevent earlier visitation. Evidence from Trinidad (Snow & Snow, 1971) suggests that tanagers and honeycreepers depend on nectar for only a small portion of their diets. Green honeycreepers, for example, were observed eating fruit during 63% of the feeding observations and fed on nectar only 22% of the time. Even bananaquits, which were observed to feed primarily on nectar (76% of the observations), supplemented their diets with fruit and insects (Snow & Snow, 1971).

Erythrina megistophylla clearly fits the "perching" or passerine bird pollination syndrome as presented by Cruden & Toledo (1977) for New World species and by Faegri & van der Pijl (1979) for Old World species. Although it is also pollinated by passerine birds, the main visitors to *Erythrina megistophylla* were honeycreepers (Coerebidae) rather than orioles (Icteridae) as was found for *E. breviflora* by Cruden & Toledo (1977). This probably reflects the very different communities in which these two species occur. *Erythrina megistophylla* grows in the lowland tropical wet forests of Ecuador, while *E. breviflora* is found in drier oak and pine-oak woodland between 1,200 and 2,300 m in Mexico.

Flower orientation appears to play an important role in bird-pollinated flowers (Stiles, 1978). The inflorescence axis of *Erythrina megistophylla* provides an excellent perch for birds visiting the backwardly directed, short-tubed flowers (see Figs. 4–5). Its flower orientation, while convenient for perching birds, makes hummingbird visitation awkward. Since hummingbirds do visit these flowers, it is hard to know whether the positioning of flowers actually results in a reduction of foraging efficiency. It may be that the vertically oriented raceme of hummingbird-pollinated *Erythrina* species evolved more as a means to exclude other visitors than as a response to maximize hummingbird foraging efficiency.

As suggested by Toledo (1977), passerine birds do seem to play a larger role in the pollination of New World plant species than previously suspected. Passerine flower visitors that may be legitimate pollinators have been reported by Alvarez del Toro (1963), Johow (1898), Leck (1974), Raven (1974), Schemske

(1975), Toledo (1975), and Cruden & Toledo (1977), in addition to Feinsinger et al., Morton, and Toledo & Hernández, all this symposium. In many instances where passerine birds are common visitors, it is difficult to evaluate their pollination efficacy (Baker et al., 1971; Toledo, 1977). *Ceiba pentandra* (L.) Gaertn. (Toledo, 1977) provides an example of such a situation. It is adapted primarily to bats but is heavily visited by passerine birds, in addition to hummingbirds, insects and four types of mammals (Toledo, 1977). Only through more detailed experimental analyses of pollen transfer effectiveness and stigma receptivity will it be possible to unravel the selective pressures exerted by various visitors in these situations. It is likely that more detailed studies will undoubtedly ascribe a greater importance to passerine birds for pollen dispersal in plants which they are already known to visit and will also reveal additional plants specifically adapted to passerine bird pollination.

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ERYTHRINA OLIVIAE: A NEW CASE OF ORIOLE POLLINATION IN MEXICO[1]

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ABSTRACT

Erythrina oliviae, a dry-season-flowering tree from Mexico, is primarily pollinated by perching passerine birds. Other pollinators have also been noted. The nontubular flowers are directed to the ground, and the keel and wings function as nectar containers. The perch is vertical. The flowers produce large amounts of nectar, which contains a low percentage of sugar and a high number of amino acids.

It is possible to recognize two basic patterns in the flower structure of genus *Erythrina* (Leguminosae): (1) the standard enormously elongated and the keel and wings reduced to minimal size, and (2) the standard ovate or obovate and the keel and wings more or less conspicuously exserted from the calyx. In the first case the flower takes a decidedly tubular shape, and in the second it assumes a more generalized gaping configuration. A general correlation between these flower structures and pollination types may be also assumed. In the first case, the flowers can apparently be visited and pollinated efficiently only by hummingbirds,[3] and all the species, except the small African sect. *Humeanae* Barneby & Krukoff, with this kind of flower are from the New World (Raven, 1974, 1977; Toledo, 1974). In the second case the flowers are generally adapted to perching-bird pollination (Docters van Leeuwen, 1932; Singh, 1929; Ali, 1932), although they are also visited by hummingbirds, insects, squirrels and bats (Raven, 1977) and are predominantly, but not exclusively, from the Old World. In fact, a review of Krukoff & Barneby's (1974) conspectus of *Erythrina* shows that although the majority of American species (55) have tubular flowers and are therefore hummingbird pollinated, there are also a few species (12) with more generalized flowers (Table 1). The studies of pollination biology in this second group of species are very relevant because in it are included the species of subgen. *Micropteryx*, which has been considered the most primitive of the genus, and therefore perching-bird pollination in America may be considered an archaic syndrome which apparently preceded pollination by hummingbirds. At present, the data that have appeared about the pollination of American species of *Erythrina* with nontubular flowers seem to indicate that in this group both passerine bird pollination and hummingbird pollination is possible. They suggest

[1] We are grateful to M. Sousa for providing information about the species studied. We wish to thank M. Campomanes for amino acids analysis of nectar, L. Herrera who made the illustrations, and Alfonso Delgado for reading the manuscript. Finally we are especially grateful to Dr. Peter H. Raven for encouragement and for providing information, and Dr. Rupert Barneby for critically reading the manuscript.

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[3] The following may be an exception; although van der Pijl (1937) proposed a possible disharmony between Asiatic flower-birds and American bird-flowers, Doctors van Leeuwen (1932; 93) refers to the case of the Venezuelan *Erythrina* (*E. umbrosa* H.B.K. which is a synonym of *E. mitis* Jacquin) which is cultivated in Java and visited by three species of sunbirds.

ANN. MISSOURI BOT. GARD. 66: 503–511. 1979.

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TABLE 1. American species of *Erythrina* with nontubular flowers.

Taxon	Distribution
Subgen. *Micropteryx* (Walpers) J. G. Baker	
E. fusca Loureiro	Pantropical
E. crista-galli L.	Uruguay, Argentina, Paraguay, Brazil, Bolivia
E. falcata Bentham	Argentina, Paraguay, Brazil, Bolivia, Peru
E. poeppigiana (Walpers) O. F. Cook	Bolivia, Brazil, Peru, Ecuador, Colombia, Panama
E. verna Velloso	Brazil, Bolivia
E. ulei Harms	Brazil, Bolivia, Ecuador
E. dominguezii Hassler	Brazil, Paraguay, Bolivia, Argentina
Subgen. *Erythrina*	
E. breviflora A. DC.	Mexico
E. edulis Triana	Peru, Colombia, Ecuador, Venezuela
E. oliviae Krukoff	Mexico
Subgen. *Erythraster* Barneby & Krukoff	
E. velutina Willd.	Brazil, Ecuador, Colombia, Venezuela, Antilles
E. grisebachii Urban	Cuba

that pollination by hummingbirds in *Erythrina* is not limited to tubular flowers. Thus, the studies by M. Duncan in *E. fusca* (Raven, 1974) and in *E. breviflora* (Cruden & Toledo, 1977) have demonstrated that the flowers of these species are visited and pollinated by orioles and other passerine birds. In *E. poeppigiana*, on the other hand, hummingbirds are frequent (Snow & Snow, 1972; Raven, 1977), although the primary visitors are orioles and other perching birds (Skutch, 1954; Snow & Snow, 1971; Timkin, 1970; Feinsinger et al., this symposium). Finally, some casual reports (Stiles, 1973; Pickens, 1931) indicate that *E. crista-galli* is visited at times and apparently pollinated by hummingbirds. In this paper, the pollination of another American species of *Erythrina* with nontubular flowers is described and discussed: *E. oliviae*. The voucher for this species (*H. M. Hernández* 2), as well as other vouchers for species mentioned in this paper, were verified by B. A. Krukoff and are deposited at MEXU and NY.

STUDY SITES AND METHODS

Erythrina oliviae is a tree endemic to central Mexico where it has been collected only in restricted areas of the Río Balsas depression. This species is called "zompantle," and occurs particularly along the streams of pronounced slopes. Flower visitors and their behavior were studied in April and May of 1978 in three localities: El Papayo (between Izúcar de Matamoros and Acatlán) and Chinantla, both in Puebla, and Infiernillo in Michoacán (Fig. 1A). The two first localities are situated in the easternmost portion of the depression (high Balsas), while the third is on the west of it (low Balsas). All the sites have a very dry and hot climate, with an annual precipitation between 650 (Acatlán) and 490 mm (Infiernillo) and an annual average temperature between 24.6 (Acatlán) and 29.6°C (Infiernillo). There is a pronounced dry season from

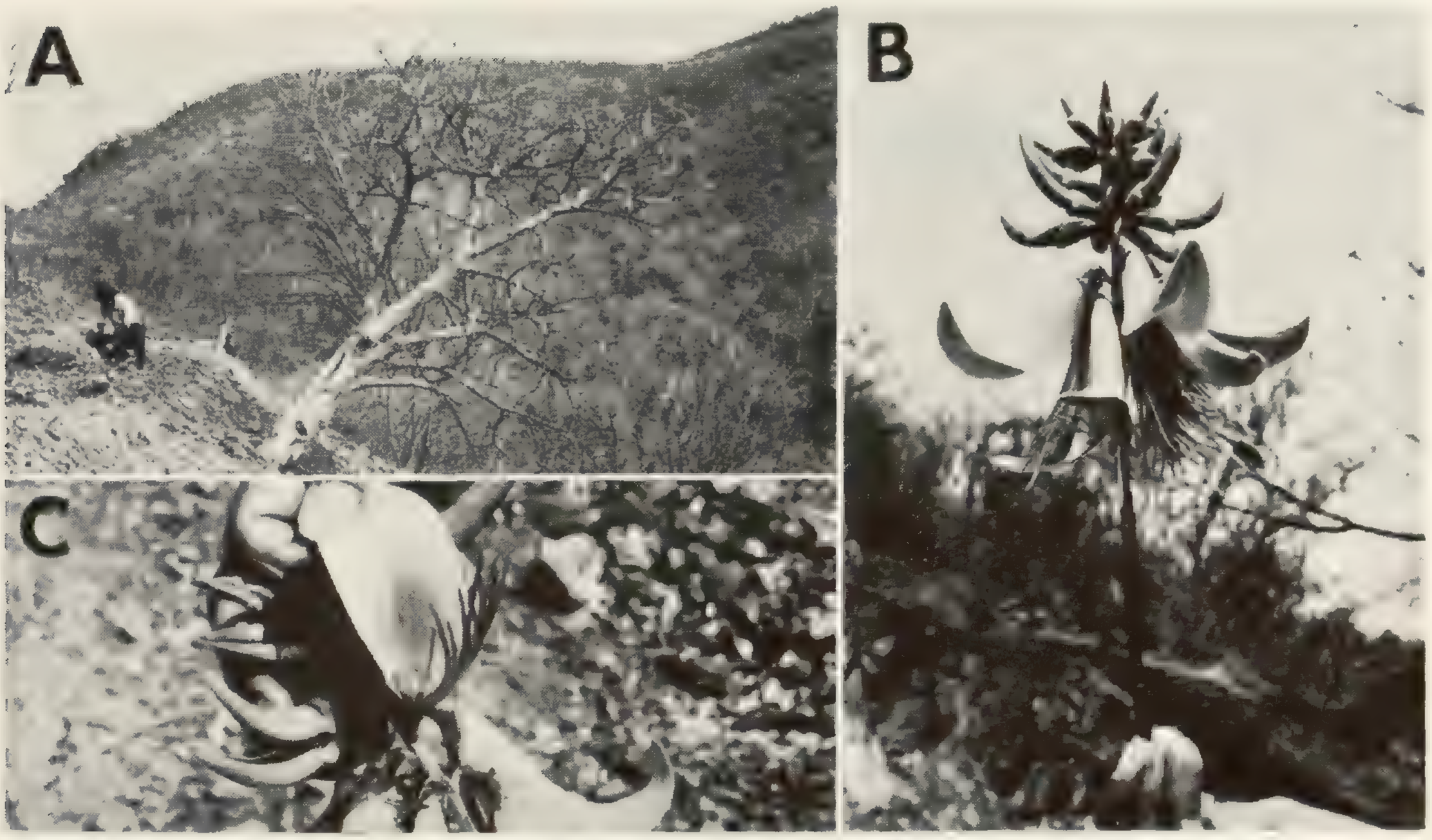

FIGURE 1. *Erythrina oliviae*.—A. A tree in the Infiernillo region.—B. Inflorescence.—C. Flower showing the sexual parts. Note the form of the keel and wings.

November to mid-May. All the sites are covered by tropical dry forests, with plants such as *Bursera* spp., *Pseudosmodingium perniciosum* (H.B.K.) Engler, *Ceiba parvifolia* Rose, *Lysiloma microphylla* Bentham, *Ipomoea* spp., *Pithecellobium dulce* (Roxb.) Bentham, *Prosopis juliflora* (Swartz) A. DC., and cacti such as *Lemairocereus*, *Cephalocereus* and *Myrtillocactus* (Miranda, 1947).

Nectar volumes were measured with calibrated micropipets and sugar concentrations with an Erma Hand Refractometer. The identification of amino acids in the nectar was made by M. Campomanes of Instituto de Investigaciones Biomédicas, UNAM, using an Aminco Flourometric Liquid Chromatography System. The nectar was removed from several flowers with a sterilized syringe and immediately refrigerated. Only nectar from the El Papayo population was taken for the amino acids identification.

FLOWERING TIME AND FLOWER CHARACTERISTICS

Like many other species of *Erythrina*, *E. oliviae* flowers towards the last part of the dry season (mid-April to mid-June). The inflorescence is an erect raceme 20–30 cm long (Fig. 1B). Each inflorescence has from 40 to 80 flowers which are directed downwards. The standard is very large (9 cm long × 3 cm wide when open) and of a bright to pale orange color; the very reduced keel and wings form a compact concavity for the nectar and are colored bright reddish orange (Fig. 1C). The stamens are arranged in three ranks of different length, and the pistil lies in the center of them. This species is very noticeable from long distances when it is in bloom. An estimate made in a tree at Infiernillo gave a total of 350 inflorescences.

TABLE 2. Some characteristics of nectar of *Erythrina oliviae*.

Flower	High Balsas (El Papayo, Puebla)		Low Balsas (Infiernillo, Michoacán)	
	μl/flower	% Sugar/ flower	μl/flower	% Sugar/ flower
I	220	11.74	170	11.32
II	230	11.68	210	11.40
III	260	11.76	270	11.40
IV	250	12.03	260	11.57
V	230	11.72	100	11.57
VI	225	11.60	280	10.77
VII	220	11.56	270	10.77
	x̄ 233.5	11.72	222.8	11.30

NECTAR PRODUCTION AND CONSTITUENTS

The analysis of nectar sampled for two populations of *Erythrina oliviae*, one in the high Balsas and the other in the low Balsas (Table 2), shows that the flowers produce extremely large volumes of nectar with a low percentage of sugar. It is interesting that the results are very similar, both between flowers and between populations. A total of 20 amino acids were identified in the nectar of *E. oliviae* (Table 3). Of these, the most abundant are glutamine (39.68% of the total amount), aspargine (14.58%), and lycine (9.21%). Amino acids constitute 22.91 μmol per ml of nectar; this means that on the average each flower has approximately 5.35 μmol of amino acids.

TABLE 3. Amino acids content in the nectar of *Erythrina oliviae*.

Amino Acids	μmol/ml	Proportion (%)
Alanine	.03	.13
Arginine	.02	.08
Aspargine	3.34	14.58
Aspartic Acid	1.33	5.80
Glutamic Acid	1.62	7.07
Glutamine	9.09	39.68
Glycine	.27	1.18
Hypotaurine	?	?
Histidine	1.05	4.58
Isoleucine	.08	.35
Leucine	.05	.22
Lycine	2.11	9.21
Methionine	1.50	6.55
Ornithine	?	?
Serine	1.31	5.72
Threonine	?	?
Tryptophane	?	?
Tyrosine	.21	.92
Valine	.39	1.70
Phenylalanine	.51	2.23
Total	22.91	100.00

TABLE 4. Number of foraging visits recorded for each species of perching bird taking nectar from *Erythrina oliviae*.

Bird Species	Hours of Observation/Number of Observed Trees		
	El Papayo (4 h/10)*	Chinantla (1 h 30′/5)	Infiernillo (3 h 5′/12)
Icteridae			
Icterus sclateri	36	9	8
I. wagleri	—	3	—
Tangavius aeneus	—	1	—
Troglodytidae			
Campylorhynchus bruneicapillus	8	—	—
C. rufinucha	—	—	4
Picidae			
Centurus hypopolius	8	—	—
Fringillidae			
Pheucticus chrysopeplus	7	—	—
Parulidae			
Unidentified	—	—	1

FLOWER VISITORS

Observations of the flower visitors of *Erythrina oliviae* were made at 27 trees in 3 localities. The approximate total time of observation was 8.5 hours, which included censuses at all hours of the day. A total of 8 species of passerine birds in five families were seen taking nectar (Table 4). In addition, a few individuals of three species of hummingbird (*Amazilia viridifrons* and two unidentified), carpenter bees (*Xylocopa* sp.), and domestic honeybees (*Apis mellifera*) were noted as occasional visitors to the flowers of *E. oliviae*. The perching birds were observed at each study site and were undoubtedly the primary flower visitors. Of these, the orioles, which made 60, 90, and 60%, respectively, of the observed visits to the flowers of the three populations studied, were the primary pollinators. In order to take the nectar, the perching birds approach the flowers of *E. oliviae* in two ways: using the peduncle or a branch as a perch and reaching the flowers from beneath (Fig. 2A), or by perching on the top of inflorescences and inclining the head downwards so as to plunge the beak into the flower (Fig. 2B). The first type of visit seems to be more simple and involves less effort, while the second requires more acrobatic ability. All the perching birds observed taking nectar from *E. oliviae* used the first method, but only the two species of oriole (*Icterus sclateri* and *I. wagleri*) were also observed visiting the flowers in the second way. In the first case the bird's throat or breast is coated with pollen and in the second its crown or forehead. Of the perching birds it was the orioles and, secondarily, the wrens who more easily foraged at the flowers of *E. oliviae*. Since the nectar is concealed by the keel and the wings, it is only accessible to birds with elongated bills. At El Papayo we observed the yellow grosbeak (*Pheucticus chrysopeplus*) destroying the standard and perhaps the keel and

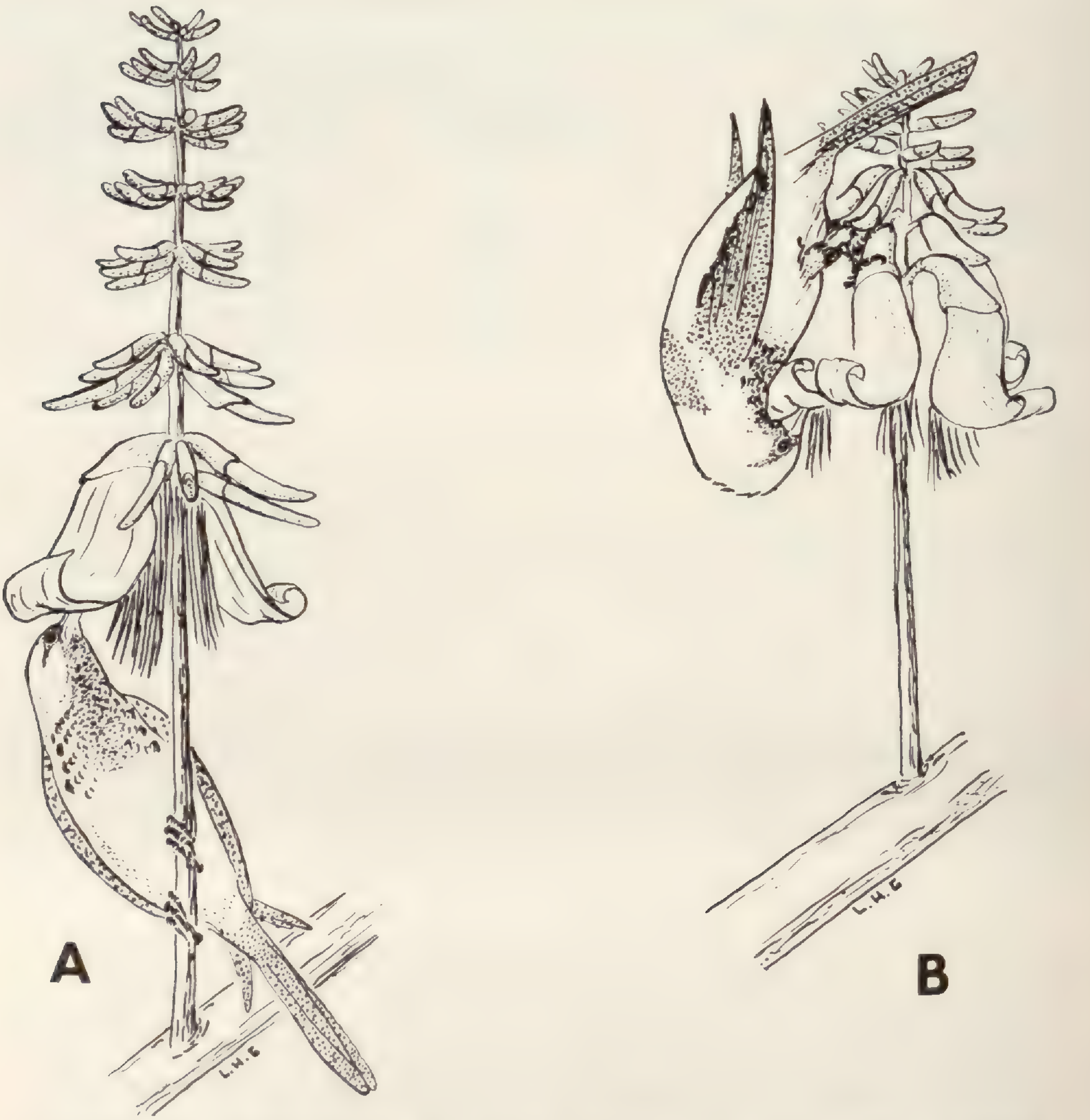

FIGURE 2. The two modalities of foraging visitation of perching birds to flowers of *Erythrina oliviae* (see text).

wings in order to rob the nectar. It is interesting also that while we were at El Papayo the local woodpecker (*Centurus hypopolius*) was a notable visitor of *Erythrina*, but the very abundant woodpecker of the El Infiernillo region (*Centurus chrysogenis*) ignored the flowers of this species completely. In contrast to the passerine birds, hummingbirds were less abundant visitors to the flowers of *E. oliviae* with 3, 8, and 7 visits recorded for the three populations studied. The downwardly directed flowers and the inflorescence structure make foraging by hovering hummingbirds quite difficult. We observed hummingbirds visiting the flowers using the stamens as a perch or piercing the corolla and robbing the nectar. Finally, the carpenter bees and honeybees were observed collecting pollen at the two first hours of the day, after which they disappeared.

Discussion

Excepting the vertical orientation of the inflorescence, all the floral characteristics of *Erythrina oliviae* are consistent with those hypothesized by Cruden & Toledo (1977) as suited to perching-bird pollination. In fact, the hypothesis that oriole-pollinated flowers are of the gaping type and have higher amounts of nectar, lower levels of sugar, and higher numbers of amino acids than the hummingbird-pollinated flowers is confirmed by the results of this paper. Unfortunately, no analysis of ratio of sugars was made in *E. oliviae*, so that it is not possible to test the less "sucrosophilous" condition of the nectar of oriole-pollinated flowers as suggested by the same authors. In relation to the amount of nectar, *E. oliviae* is the species that is known to produce the largest volumes per flower.[4] This may be a direct result of the size of the flower but is also a strategic response of the plant to the drastic climate conditions that prevail within its distributional range. The flowering period of *E. oliviae* coincides with the most severe period of the year when maximal temperatures between 38 and 42°C coincide with extremely low rainfall. Under these conditions water is an extremely scarce resource for animals so that the enormous quantities of nectar provided by *E. oliviae* may attract birds as much by its water content as by its nutritional value (represented by sugars and amino acids). The repeated visits of the birds to the flowers of *E. oliviae* at all hours of the day would indicate this. Twenty amino acids were found in the nectar, including those necessary for growth and maintenance of birds (Fisher, 1972). It is interesting to note that the number of amino acids in *E. oliviae* nectar is higher than that found by Cruden & Toledo (1977) in *E. breviflora* (18 amino acids) and by Baker (1976) in *Jacaratia dolichaula* (J. D. Smith) Woodson (10) and *Carica papaya* L. (9).

It is interesting to note the functions of the keel and wings as nectar containers. Since the flowers are directed to the ground, the keel and wings prevent the nectar from draining off and, in addition, they protect it from desiccation or evaporation induced by the high temperatures of the environment. Moreover, the attractive red color of the inner petals contrasts with the orange of the standard and must operate as a nectar guide to the birds, a very unusual character in ornithophilous flowers (Faegri & van der Pijl, 1971). Finally, the disposition of the keel and wings as a closed container for the nectar must facilitate the visit of orioles and discourage that of other perching birds, since orioles habitually thrust the bill into the closed flower, thereby giving the brushy tongue access to the food (Beecher, 1950).

Erythrina oliviae is the first American perching-bird pollinated species in which the perch has been noted to be vertical. In all described cases of perching-bird pollination in America, which include *Erythrina breviflora* (Cruden & Toledo, 1977), *Bernoullia flammea* Oliver (Toledo, 1977), *Chiranthodendron penta-*

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[4] Other species of *Erythrina* with large volumes of nectar per flower are two oriole-pollinated species: *E. fusca* (114 μl) (Duncan, unpublished) and *E. breviflora* (64 μl) (Cruden & Toledo, 1977) and one pollinated by hummingbirds, *E. leptorhiza* (42 μl), (Hernández & Toledo, this symposium). However, no species produces more nectar than *E. oliviae*.

dactylon Larreategui (Toledo, 1975), *Combretum farinosum* H.B.K. (Alvarez del Toro, 1963) and *Puya chilensis* Molina (Johow, 1910), birds use horizontal perches in order to obtain the nectar. This particular characteristic of *E. oliviae* probably is a consequence of its African links. In fact, the close resemblance of the flowers of *E. oliviae* to those of some South African species of the genus, and particularly with *E. caffra* Thunberg (Krukoff & Barneby, 1974), suggests that the vertical perch in *E. oliviae* may be a relictual character common to it and relatives now in Africa, where the acrobatic sunbirds are the primary pollinators. In this connection it may be noted that there is much similarity in structure between the inflorescences of *E. oliviae* and *Aloe* spp., an African group of plants adapted to sunbird pollination (Skead, 1967). Thus, *E. oliviae* offers an American example of passerine-bird pollination in which the perch is in a vertical position, whereas *E. breviflora*, which is taxonomically near to the Asiatic sections *Suberosae* Krukoff, *Arborescentes* Krukoff, and *Hypaphorus* (Hasskarl) Krukoff, is of the type where the passerine birds use horizontal perches during the visits to the flowers. Moreover, it is possible to predict from flower structure a similar pattern for two other American species, *E. velutina* and *E. grisebachii*, placed by Krukoff & Barneby (1974) in the predominantly paleotropical sect. *Erythraster*. Similarly, in *E. edulis*, another American species whose flowers are essentially the same as those of *E. breviflora*, an horizontal perch must be expected. This distinction in the passerine-bird pollination (horizontal perch versus vertical perch) should be investigated in the future because it surely is related to behavioral differences of the groups of birds during the foraging. Finally, passerine-bird pollination by a vertical perch seems to be in an evolutionary sequence nearer to pollination by hummingbirds than that of passerine birds using an horizontal perch, since the inflorescence resembles in structure one that is normally hummingbird pollinated.

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THE ROLE OF NECTAR ROBBERS AND POLLINATORS IN THE REPRODUCTION OF *ERYTHRINA LEPTORHIZA*[1]

HÉCTOR M. HERNÁNDEZ[2] AND VÍCTOR MANUEL TOLEDO[2]

ABSTRACT

The pollination ecology of *Erythrina leptorhiza* is discussed. Flowering takes place synchronously during the rainy season. The species is self-incompatible and produces some flowers with short styles. The flowers are adapted for hummingbird pollination in their morphology and high nectar production early in the day. Of four bird visitors, three were nectar robbers (89% of the total foraging visits) and one was a legitimate, traplining pollinator (11% of the foraging visits).

All species of the genus *Erythrina* are bird pollinated (Raven, 1974, 1977; Toledo, 1974). Although most American species are pollinated by hummingbirds (Toledo, 1974), there are reports of nonspecialized passerine birds visiting *Erythrina* on this continent (Skutch, 1954; Timkin, 1970; Snow & Snow, 1971; Leck, 1974; Raven, 1974; Cruden & Toledo, 1977; Toledo & Hernández, this symposium). Although there are numerous observations about hummingbirds visiting species of *Erythrina* (see Toledo, 1974: table 1), detailed studies of pollination by hummingbirds in this genus have been initiated only recently (Toledo, 1974; and many others). The present study of *E. leptorhiza* A. DC. was made because of our ignorance of its pollination ecology, and because it shares characteristics of both perching- and hummingbird-pollinated species. As pointed out by Krukoff & Barneby (1974: 362), it shows affinity with the sympatric *E. breviflora* A. DC. (perching bird-pollinated, Cruden & Toledo, 1977) in habitat, pod and seeds. Furthermore, "the very high amounts of amino acids in many samples of seeds of *E. leptorhiza* suggest affinities with species of sect. *Breviflorae* and *Edules*" (Romeo, 1973: 65; quoted by Krukoff & Barneby, 1974: 363). In this paper an account is given of the pollination ecology of *E. leptorhiza*, and the role played by its visitors is discussed in the light of flowering phenology, flower characteristics, and breeding system.

STUDY AREA AND METHODS

Erythrina leptorhiza is endemic to temperate elevations (±1,800–2,700 m) in southcentral Mexico, ranging from the southern edge of the Central Plateau through the Transverse Volcanic Range to Puebla (Krukoff & Barneby, 1974: 362). It is characterized by its herbaceous habit of growth and is usually found in a secondary succession in the oak and pine-oak forest. This perennial herb

[1] We are grateful to Alfonso Delgado for reading the manuscript. We also want to thank Luis Herrera for the illustrations and Alina Chacón for her work with us in the field. We are especially grateful to Dr. P. H. Raven for encouraging us to study *Erythrina* species and to Dr. Rupert Barneby for critically reading the manuscript. The vouchers for *E. leptorhiza* A. DC. (*Grupo Etn. 192*) are deposited at MEXU and NY. The collection has been checked by B. A. Krukoff.

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has the ability to reproduce itself vegetatively by rhizomes. The individual plants die back to soil level each year before the dry winter season and grow in the following wet season to become reproductive by seed again.

Our field observations were made primarily in a deciduous forest situated 51 km SE of Mexico City, Morelos, on the road between Xochimilco and Oaxtepec, during June and July 1978. The site is noted for the high number of *Erythrina leptorhiza* plants, probably as a result of fire in this part of the forest.

For a quantitative evaluation of flowering and setting of the fruit, we made some counts on 25 randomly selected plants at regular intervals. Nectar volumes were measured with calibrated micropipets (10 μl) from freshly opened flowers, before the nectar had time to become more concentrated by evaporation and before it could be removed by floral visitors. At the same time, we measured the sugar concentration with an Erma Hand Refractometer, model A. Presence of floral dimorphism was determined by style and stamen measurements for several individual plants. Measurements were made in the laboratory on previously fixed flowers in anthesis. The size of ovules and pollen grains was determined by microscopic examination and measurements. Controlled artificial pollination experiments employing the techniques of Bawa (1974) were carried out to test for self-compatibility.

Flowering Phenology and Fruit Set

Like *Erythrina breviflora* (Cruden & Toledo, 1977), *E. leptorhiza* flowers during the rainy season and is leafy at anthesis, in contrast to the flowering strategy of many other Mexican species of *Erythrina*. Field observations indicates that almost all the individuals begin to flower synchronously as early as mid-May, ending in the second half of August. This is in accordance with data on herbarium sheets.

Figure 1 shows a partial account of flowering dynamics. The solid line indicates the number of opened flowers, and the broken line indicates the fruit set (percent of flowers that develop into fruit). It is important to mention that fruit set was calculated independently for three different periods of time (see Fig. 1). Thus, fruit production begins almost at the final phase of flowering. Then, its rate of production increases. In other words, fruit set is increasing while the number of available flowers decreases.

Inflorescence, Floral Morphology, and Nectar Production

Contrasted with the species which flower during the dry season and have compact racemes, the inflorescence of *Erythrina leptorhiza* is an elongated raceme (Fig. 2A). The flower stalks usually grow singly and each has an accompanying branch of leaves. Each inflorescence has from 24 to 60 or more flowers. Its floral structure is quite similar to that of all hummingbird-pollinated species of *Erythrina*. The narrow standard is orange and encloses the sexual organs. The stamens are in four levels as they are of different lengths, thus enlarging the contact's surface with the visitor. The anthers face upwards facilitating deposition of pollen

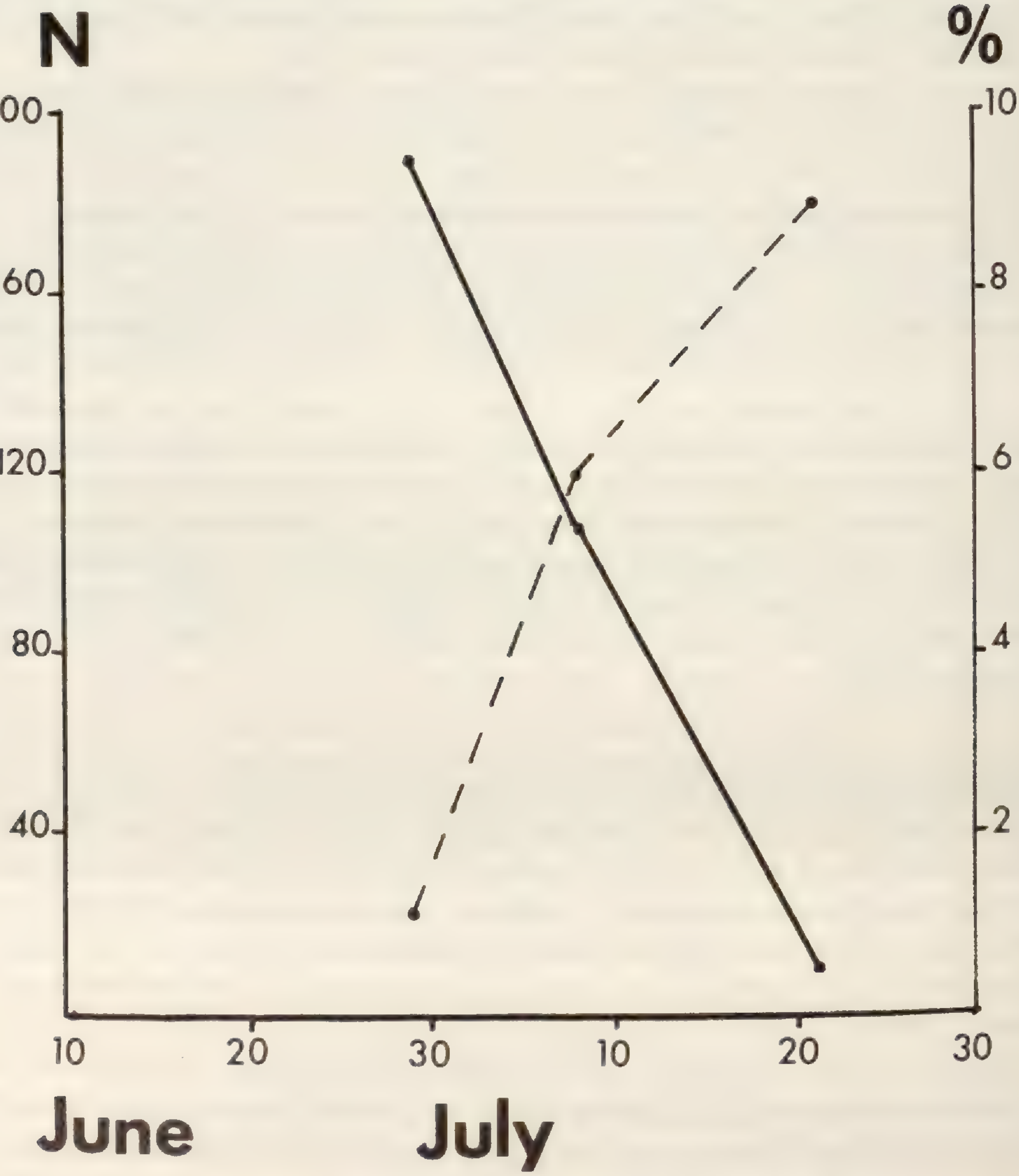

Figure 1. Final phase of flowering and setting of fruit of *Erythrina leptorhiza*. N = solid line = number of opened flowers; % = broken line = percent of flowers that develop into fruit.

on the throat or bill of the hummingbird. The pistil lies in the center of the stamens. Several characteristics of the flower seem to be very variable. Thus, the corolla color varies from pale to bright orange in flowers at anthesis. Both calyx and corolla are quite variable as well, with ranges of 27–39 mm and 65–87 mm respectively. The size of the longest stamen ranges from approximately 51 to 74 mm.

The daily pattern of nectar production of *Erythrina leptorhiza* is similar to many hummingbird-pollinated species of plants. Thus, there is a very high nectar production in the early morning [42.5 (33–50 μl][3], then a rapid decline to low levels by afternoon. The sugar density is 22.7%, ranging from 21.7% to 23.5%.

FIGURE 2. *Erythrina leptorhiza*.—A. Inflorescence.—B. Detail of inflorescence showing the holes made by *Diglossa baritula* on the calyx.—C. Perforate calyx with a drop of nectar.

TABLE 1. Morphology of the floral forms in *Erythrina leptorhiza*.

	Long Styles	Short Styles
Style length (mm)[a]	58 (48–69)	23 (18–35)
Number of ovules[a]	7.4 (3–10)	10.6 (7–12)
Ovule size(μ)[b]	893.5 × 728.5	602.8 × 480.4
Pollen grain size (μ)[b]	31.7 × 27.5	27.5 × 24.7

[a] Mean and range.
[b] Mean.

BREEDING SYSTEM

In our population we found two types of flowers: (1) with long styles; and (2) with short styles. The stamen lengths are the same in both kinds of flowers ($\bar{x}$ = 61 mm in the longest stamen), although there is dimorphism in other floral parameters (Table 1). In the long-styled flowers the anthers are just in front of the stigma, while in the short-styled ones the stigma does not come in contact with the anthers. In these there is a dimorphism in both ovule and pollen grain sizes, and the average number of ovules is different as well. In short-styled flowers the styles are incurved at the tip, through 90°, so the stigma is oriented toward the standard. By contrast, those of the long-styled flowers are completely straight.

The long-style flowers constituted 82.8% of our sample (N = 64), the remainder being of the short-style flowers. Nevertheless, we do not know the real proportion of each flower form in the population.

Investigation of the breeding system indicates self-incompatibility in *Erythrina leptorhiza*. We found two cleistogamic flowers on a long-styled plant. These flowers with nondeveloped corollas were able to produce fruit.

VISITORS: NECTAR ROBBERS AND POLLINATORS

We were able to identify four species of birds visiting the flowers of *Erythrina leptorhiza* (Table 2). These birds fall into two groups: the nectar robbers that take the nectar by illegitimate foraging, and the pollinators. The Mexican flowerpiercer (*Diglossa baritula*) was observed robbing the nectar by perforation of the calyx (Fig. 3A). The functioning of the mandibular mechanism of *Diglossa* during the process of perforation and feeding has been described by Lyon & Chadek (1971). Apparently, perforation of *E. leptorhiza* flowers by *D. baritula* is very easy, probably because of the thin-chartaceous texture of the calyx. The high percentage of opened flowers with holes (91.5, 100, and 100% in three different counts) reflects the preference of this nectarivorous bird for the flowers of *E. leptorhiza* (Figs. 2B–2C). In the same group fall two species of hummingbirds of moderate size: *Amazilia beryllina* and *Hylocharis leucotis*. The approach of these hummingbirds to the flowers of *E. leptorhiza* is quite different from that

[3] Mean and range (μl).

TABLE 2. Number of foraging visits recorded for species of birds visiting flowers of *Erythrina leptorhiza*.

Species	Date and Length of Observation		
	16/VI/78 (1 h)	29/VI/78 (6 h)	8/VII/78 (3½ h)
Amazilia beryllina	4[a]	18	4
Hylocharis leucotis	—	7	11
Lampornis clemenciae	1	3	3
Diglossa baritula	—	5	7

generally observed in most *Erythrina* species (Toledo, 1974). They take the nectar by plunging the beak into the calyx, but from the external side of the standard (Fig. 3B). As the hummingbird's beak does not enter into contact with the anthers, obviously there is no effective pollination. The degree of mutual aggressiveness between hummingbirds and *D. baritula* is considerably less than among different hummingbirds and conspecifics. In most cases hummingbirds and *D. baritula* ignore each other; nevertheless, we observed some threat displays of the flower-piercer towards *A. beryllina*.

The large blue-throated hummingbird (*Lampornis clemenciae*) is the one species that exploits the nectar in a legitimate way. Contrasted with the above-described style of hummingbird visitation, this species goes into the calyx, where the nectar is deposited, from the inner side of the standard (Fig. 3C). The bird's head remains a short time between stamens and standard, and, as a consequence, its bill and throat become coated with pollen. The "trapline" was the general feeding strategy of *L. clemenciae*. Birds of this species travelled between clumps of flowers following a regular route. We checked on the fruit production in a place where *L. clemenciae* was a systematic visitor, and it was higher than elsewhere in the area (fruit set = 16.14).

Lucifer hummingbird (*Calothorax lucifer*) was a common visitor of *Fuchsia microphyla* H.B.K. and other ornithophilous flowers of the forest but was never seen drinking the nectar of *Erythrina leptorhiza*. Hummingbirds usually utilized alternative nectar sources, e.g., *Bouvardia ternifolia* (Cav.) Schlecht., *Calliandra grandiflora* (L'Her.) Bentham, *Castilleja canescens* Bentham, *Penstemon campanulatus* Willd., *Psittacanthus schiedeanus* (Schlect. & Cham.) Blume ex Schult., and *Spiranthes aurantiaca* (Llave & Lex.) Hemsley.

DISCUSSION

The results obtained from the observations are very suggestive. It is possible to limit the discussion to the following three aspects: (1) the variability of the flowers, (2) the role played by the flower visitors in the breeding behavior of *Erythrina leptorhiza*, and (3) the relationship between flower dynamics and fruit set.

The floral structure of *Erythrina leptorhiza* is quite variable. Flowers with short styles are distinct in the orientation of the stigma, number of ovules, and

FIGURE 3. The three modalities of bird visitation to the flowers of *Erythrina leptorhiza*.—A–B. Illegitimate visits by *Diglossa baritula* and hummingbirds of moderate size, respectively; C. *Lampornis clemenciae* visiting the flowers in a legitimate way.

both ovule and pollen grain size. Experimental results indicate self-incompatibility, although two cleistogamic flowers were found in a single population. This suggests that self-incompatibility is not absolute in the population. However, the contribution of cleistogamic flowers to the seed pool is insignificant because of their rarity. Our knowledge of the breeding system is limited, and it needs more research.

Following the nomenclature of Barrows (1976) the visitors of *Erythrina leptorhiza* are categorized as nectar-foraging-perforating robbers, nectar-foraging robbers, and pollinators. *Diglossa baritula* bites holes in the corolla and robs the nectar. Although the total number of foraging visits of this species was not higher than that of the other visitors (19.0% of the total), the high proportion of perforated *E. leptorhiza* flowers indicates that the flower-piercer plays an important role in depleting nectar resources. Two hummingbird species (*Hylocharis leucotis* and *Amazilia beryllina*) are also considered as nectar robbers. These two species account for approximately 70% of the total visits. As described above, these two hummingbirds do not pollinate flowers of *E. leptorhiza*, and it is difficult to account for it. However, it is possible that, due to their moderate size, the approach of these hummingbirds to the flowers becomes easier from the outside of the standard. The smallest hummingbird, *Calothorax lucifer*, commonly seen in the forest never visited *E. leptorhiza*. Finally, although the large hummingbird *Lampornis clemenciae* was the one species that took the nectar in a legitimate way, it was characterized by its low frequency of visits (11.1%). In sum, the nectar robbers represent 89% of the total foraging visits recorded and the effective pollinators only 11.1%.

Bird-pollinated flowers generally produce large quantities of nectar (Grant & Grant, 1968; Faegri & van der Pijl, 1971), and a copious amount of nectar available may favor territoriality (Stiles, 1975). Since *Erythrina leptorhiza* grows in large clumps and shows high synchronism in time of blooming, it appears preeminently adapted to pollination by territorial hummingbirds. Linhart (1973) has pointed out that hummingbird territoriality can greatly decrease pollen flow, and this may be disadvantageous to the self-incompatible *E. leptorhiza* clumps. Nevertheless, we have found that the feeding strategy of *Lampornis clemenciae* is traplining. The nectar robbers deplete the nectar resources, and, therefore, the available amount of nectar of a single clump does not satisfy the food requirements of this hummingbird. As a result, *L. clemenciae* does not restrict its visits to the flowers of a single clump owing to the depletion by the robbers of the caloric reward presented in the flowers. Therefore, we must consider that nectar robbers may have a positive effect on the reproduction of this plant species. Observations made on the red clover (Hawkins, 1961), and on *Penstemon kunthii* C. Don (Lyon & Chadek, 1971) also reveal that nectar robbing may not be deleterious.

The relatively high amount of nectar in *Erythrina leptorhiza* (42.5 μl per flower) in comparison with other hummingbird-pollinated species of the genus, e.g., *E. coralloides* A. DC. with 9.8 μl (Cruden & Toledo, 1977), encourages exploitation by the four bird species that visit it.

The third aspect, relation between number of available flowers and fruit set, may be explained in light of the earlier discussions. The increment of fruit set which is inverse to the number of flowers open (Fig. 1) is explainable if the entire population is self-incompatible. If the number of available flowers is high, the probability of geitonogamous pollinations is high as well, and since a clump of *E. leptorhiza* is a single individual genetically, this pollination is ineffectual. By contrast, if the number of flowers open is minimal, fruit set should be maximized, because at this time the amount of nectar in a given clump is not enough to satiate the pollinator (see Heinrich & Raven, 1972, for discussion). This phenomenon sustains some of the theoretical predictions made by Cruden (1976).

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FIELD STUDIES OF SIX SOUTHERN AFRICAN SPECIES OF *ERYTHRINA*[1]

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Abstract

The *Erythrina* species of southern Africa range from small suffrutices to tall trees, up to 24 m in height. One species is a geophyte. All possess brightly colored flowers in the scarlet, crimson and orange range, while some species produce a few plants bearing cream or almost white, pink, and a variety of red flowers. All species discussed appear to produce a fair to plentiful supply of nectar, and, from observation, several species of indigenous and exotic birds are the pollinating agents. The two species of *Erythrina* sect. *Humeanae*, *E. humeana* and *E. zeyheri*, which have flowers that resemble those of the American hummingbird-pollinated species of the genus, are visited by sunbirds and white-eyes, whereas larger birds are also frequent at the flowers of the other species. The means of distribution of the usually brightly colored and poisonous seeds is unknown as yet.

Some of the southern African *Erythrina* species have been known in cultivation for a considerable period of time. *Erythrina humeana* was grown in Europe more than 150 years ago, while one species, possibly *E. caffra* or *E. lysistemon*, has been grown on the island of St. Helena for perhaps that length of time. Both these species grow easily from truncheons, and one can often see in southern Africa lines of such trees where they were once planted as protective fences or fence posts.

That so little is known of the biology of these species is therefore surprising. The following observations have been compiled from casual observations by the authors and are supplemented by information gleaned from various books (Acocks, 1975; Batten & Bokelmann, 1966; Coates Palgrave, 1977; Gledhill, 1969; Hennessy, 1972) and that supplied by Mrs. E. F. Hennessy. Careful study may, quite possibly, alter some of these observations.

Description of Species

Erthyrina acanthocarpa E. Meyer is a low (about 1.5 m) straggling, very prickly-stemmed shrub, deciduous (as are all the other species), confined to an area of dry *Cymbopogon-Themeda* grassland around Queenstown, eastern Cape Province (Fig. 1) where it grows in quantity in some places. It is subject to frost and occasional snow. The leaves, bearing hooked prickles on the veins at the back of the leaflets, appear at the same time as the inflorescences, in October–November—that is, in the southern African context, late spring. The flowers are borne on a stout peduncle produced on a short side shoot below the top of the shrub, or, less often, apparently terminally. The racemes are fairly densely packed and held

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[1] Many of the observations reported here come from Mrs. E. F. Hennessy (Department of Botany, University of Durban-Westville, Durban, South Africa) and we express our grateful thanks to her.

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in an upright or lateral position, and there are usually only one or two on each short shoot. The flowers have a green calyx and a vermilion red standard tipped with yellow lined by green veins. The minute alae are white, as are the carinal petals, but these, also small, have long, pointed pale pink tips just exceeding the calyx tube in length. The flower tends to open only slightly to expose the stamens and stigma. The brown pod (to 12 cm long or more) is densely covered with sharp prickles and contains large (20 mm diam.) brown red seeds, often attacked by the larvae of a pyraustine moth (Pyralidae).

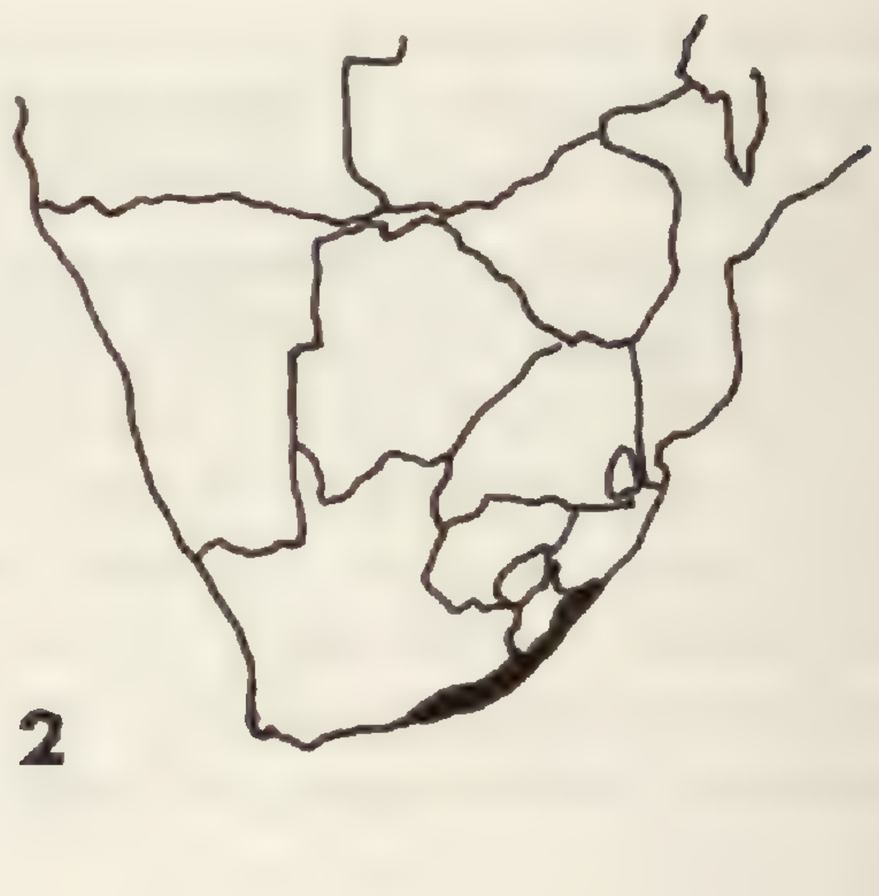
Erythrina caffra Thunberg is a tall (to 24 m) tree characteristic of coastal plain forests and temperate forests in the area from the eastern Cape Province through the Transkei to the Natal South Coast, and perhaps up into Zululand (Fig. 2). As this species and *E. lysistemon* have often been confused, the distribution may not include Zululand. This tree forms part of the canopy layer in forests. The trunk is, as with other southern African species, soft barked and light grey in color, while the wood is very porous and light, rotting readily. The leaves of each season are borne at the ends of the branches or at the tips of short side shoots and do not have hooked thorns on them, though the younger branches are armed with dark purple prickles. The leaves are subject to attack by gall-forming insects—chalcidoid hymenopterans. The flowers appear either before the leaves or with the developing leaves, in mid to late winter (July–October). They are borne in densely packed inflorescences on stout peduncles from strong shoots, usually four or five to a shoot. These heads are borne at angles from the vertical of about 45°, to horizontal, to completely upside down, i.e., 180° from upright. If horizontally placed, the flowers tend to be somewhat secund towards the upper side of the peduncle. The calyx is a velvety dark brown or dull green, the standard a rich vermilion or even crimson, the relatively small alae a greenish brown. The carinal petals are sometimes much the same color as the alae, or they may be tinged with the same red as the standard, or be, most often, purple bordered with green or orange. This is the only species among these six southern African erythrinas in which the alae and carinal petals are fully exposed, because of the very much reflexed standard in the newly opened flower. When the flower reaches anthesis, the stamens spread out in a fan shape, the style resting above them, and the flowers themselves are held almost at right angles to the peduncle. On fading, the standard resumes a position covering the other petals while the stamens and stigma project beyond the end of this petal. The pod is a dark brown, sometimes almost black organ, less than 1 cm wide and contains brilliant red orange seeds with a black hilum area. Color varieties occur occasionally. Flowers may have cream, pale pink or a variety of red shades in the standard, with corresponding alteration of the colors of the other petals. Nectar is produced in great quantity but is neither particularly sweet nor sticky. It is either colorless or slightly yellow or brown tinged. It appears as a bubble of liquid at the base of the androecial fan, held between that and the alae, and, to some extent, the carina.

Erythrina humeana Sprengel is a shrub of upright growth, reaching about 2 m in height, and occurs on forest margins from the coastal and midland areas of the eastern Cape Province through to Moçambique, including Natal, the north-eastern and eastern Transvaal, and Swaziland (Fig. 3). Except for the leaf

petioles and backs of the leaflets, it is not as prickly as the other species. The dark green leaves are, as are those of *E. caffra*, subject to attack by a chalcidoid hymenopteran parasite which produces galls. The inflorescences tend to occur at the tips of the branches, in small groups of two to four. They are held upright or may tend to a lateral or horizontal position, in which case the flowers become secund towards the upper side of the peduncle. They appear from December to May, that is, summer to late autumn, and are thus borne with the leaves already fully developed. The peduncle may reach 50 cm or more in length and may carry fully formed fruits below while still producing flowers above. This peduncle bears warty excrescences but not prickles, and is often a dull red on the flower-bearing portion, shading to green basally. The calyx is a slightly paler red than the standard or it may be tinged with green. The standard is deep scarlet fading to crimson and does not open to expose the stamens and style. The alae and carinal petals are small and pale pink. The stamens and style appear beyond the standard only as the flower fades, or sometimes not even then. The pod is slightly smaller than that of *E. caffra* and dark brown to black in color; it contains bright red seeds with a black or dark brown hilum area. The nectar is not as copious as that of *E. caffra* but seems to be sweeter and honey colored.

Erythrina latissima E. Meyer is a small tree (to 8 m) and is distributed from the eastern Cape Province through Natal, the eastern and northeastern Transvaal, Swaziland, and the higher lying parts of southern Moçambique to parts of Rhodesia (Fig. 4). The bark is very thick and corky and the trunk and branches are greater in diameter relative to their length than in the other two tree species. The wood is soft and rots rapidly when the tree dies. The large leaves are greyish green and leathery. The inflorescences appear before the leaves, during late winter into spring (September–November); they have thick peduncles. The heads are most often carried at an angle of 45° to 90° to the vertical, and there are fewer per branch than in *E. caffra* or *E. lysistemon*, comparable tree species. The calyx is red or reddish brown, densely covered with woolly hairs and tipped with five long, narrow lobes. The standard, of a deep scarlet fading to crimson as the flower withers, is spread widely and partly reflexed when the flower is open. The alae, small and concealed, are scarlet with a white margin, while the keel is greenish white tinged with scarlet. The filaments are green yellow, bearing brown anthers, and they form a fan below the gynoecium when the flower opens. The brown black pod, up to 30 cm long, holds large (to 2 cm diam.) red seeds with the usual black hilum area. Nothing is known about the nectar.

Erythrina lysistemon Hutchinson is a tree to 8–10 m tall and is the most widely distributed of the six species, occurring from the eastern Cape Province through Natal, Swaziland, the Transvaal, Botswana, Moçambique, Rhodesia, and Malawi to Zambia (Fig. 5). The trunk is dark grey, the branches are armed with numerous prickles, and, unlike *E. caffra*, the petiole and veins on the undersurface of the leaflets are also provided with thorns. The inflorescences appear in winter to early spring (August–October). They are usually laterally oriented, though a few may be at 45° to the vertical or almost upright. There is a strong tendency to subsecund arrangement of the flowers towards the upper side of the peduncle, and the flowers do not spread out away from the peduncle but lie paral-



FIGURES 1–6. Distribution of southern African species of *Erythrina*.—1. *E. acanthocarpa*.—2. *E. caffra*.—3. *E. humeana*.—4. *E. latissima*.—5. *E. lysistemon*.—6. *E. zeyheri*.

lel with it. The calyx is a dull brown or sometimes green in color, while the standard is a bright scarlet (paler shades sometimes occur) and encloses the rest of the flower almost completely, until it withers. The pod is dark brown and the seeds, comparable in size with those of *E. caffra* (about 10 mm long) are orange

red with a black hilum area. The nectar, produced in quantity, is very pale and scarcely sweet to man's taste.

Erythrina zeyheri Harvey, a geophyte or underground shrub, is distributed in scattered, isolated patches now (its former distribution is unknown) throughout an area of much higher altitude than the other species discussed. It is subject to severe frosts and snowfalls fairly regularly. It occurs in the Natal midlands, the Orange Free State and Transvaal highveld, and in the lowlands of Lesotho to at least 1,750 m altitude (Fig. 6). There is a very large underground stock (hence the name "ploughbreaker") and in spring, annual, above-ground branches are produced. These give rise to large (up to 0.5 m or more long) leaves, which bear sharp thorns on both sides of the leaflet lamina, along the veins. There is usually one inflorescence (rarely two) on each shoot, and flowering is in summer (November–January). The head of flowers is upright on a long, ribbed peduncle of the same color as the standards. The calyx is a slightly paler shade of the standard color, which is most often bright scarlet but may, in at least one population, be cream through pale to dark pink to scarlet or crimson on different plants. The alae, which are small and concealed, are scarlet (or the appropriate shade of the standard color) with a white margin, while the carina is greenish white tinged with the standard color. The stamens have green yellow filaments with brown anthers and form a fan below the gynoecium when the flower opens. The flower opens only slightly, and is borne in a dependent position, parallel with the upright peduncle. The moderately large pods are black brown and contain fairly large seeds (15 mm diam.); these are a dull red with the usual black hilum patch. A slightly sweet, pale yellow nectar is produced in moderate quantity.

Pollinators, Casual Visitors and Possible Thieves

Nothing is so far known of the possible pollinating agents of *E. acanthocarpa*, nor of its nectar.

Erythrina caffra, in the eastern Cape Province, is visited regularly in great numbers by red-wing starlings (*Onychognathus morio*). Frequent but less numerous visitors which also search the flowers are cape weavers (*Ploceus capensis*), black-headed orioles (*Oriolus larvatus*), and european starlings (*Sturnus vulgaris*), this last an introduced species which is increasing its range rapidly. Less frequent visitors but still common, are, in this area, yellow weavers (*Ploceus subaureus*), spotted-back weavers (*P. cucullatus*), forest weavers (*Symplectes bicolor*), wattled starlings (*Creatophora cinerea*), pied starlings (*Spreo bicolor*), fork-tailed drongos (*Dicrurus adsimilis*), lesser double-collared sunbirds (*Cinnyrius chalybeus*), greater double-collared sunbirds (*Cinnyrius afer*), collared sunbirds (*Anthreptes collaris*), grey sunbirds (*Cyanomitra veroxii*), black sunbirds (*Chalomitra amethystina*), cape parrots (*Poicephalus robustus*), speckled colis (*Colius striatus*), and red-billed hoopoes (*Phoeniculus purpureus*). A visitor in numbers and fairly frequent is the cape white-eye (*Zosterops pallidus*), but because of its size—it is a very small bird—it is not considered a pollinator except by chance. Bats have been observed at night around *E. caffra* trees and may possibly do some pollinating, but as the species is unknown, it may be an insect feeder

only. In Natal, *E. caffra* is visited by many of the species listed above and also by Layard's bulbul (*Pycnonotus barbatus layardi*) and Indian mynahs (*Acridotheres tristis*), an introduced bird now dominating the avian fauna in Durban and surroundings. This bird, the mynah, according to information received from Mrs. Hennessy, visits the flowering *E. caffra* in large flocks. The birds apparently not only make beak holes near the base of the standard but also nip the flowers off the peduncles, so that a shower of blossoms falls to the ground while the birds are "working" the tree. In spite of this, fruit set is good.

Erythrina humeana is visited by sunbirds in the eastern Cape, but in Natal, the cape white-eye (*Zosterops pallidus*) appears to be the most frequent visitor and the main pollinating agent, as seed is regularly set in quantity.

Erythrina latissima is reported by Mrs. Hennessy as being visited by bulbuls, mynahs, and drongos. There are probably other visitors effecting pollination.

Erythrina lysistemon is regularly visited by Indian mynahs in those parts where this bird occurs and other visitors are bulbuls, sunbirds, and fork-tailed drongos. Again, there are probably many other bird species which visit this plant and bring about pollination.

Erythrina zeyheri is found in Lesotho in areas where malachite sunbirds occur. This bird (*Nectarinia famosa*) is often seen probing the flowers for nectar and possibly insects and seed set is fairly good. Probably the same species of bird can be found on these plants in the other areas where *E. zeyheri* grows.

Erythrina crista-galli L., an introduced species often grown in public and private gardens in South Africa, has been seen by Skead to be visited for nectar by greater double-collared sunbirds and black sunbirds in the eastern Cape Province. The shape and direction of the inflorescence, the strength of the peduncle and the type of opening of the flowers (standard widely reflexed in *E. caffra*, enclosing the rest of the flower in *E. humeana*) seem all to have a close relationship to the species of indigenous birds which frequent the flowers at anthesis, but more detailed study is necessary. The quantity and quality of the nectar produced requires investigation also. Skead reports that he has noted speckled colis feeding heavily on *Aloe* nectar, then dropping further down the plant to drink water collected in the troughs of the leaves after recent rain; this shows the birds distinguish between the nectar and the rain water. No such observation has been made for *Erythrina* species, however, and this may be because the nectar produced is only slightly sweet, far less so than *Aloe* nectar. Skead also reports speckled colis (*Colius striatus*) eating (or tearing) the edges of *E. caffra* leaves.

Seed set is usually fair to good in the species of *Erythrina* discussed. These seeds can be seen in the open pods still attached to the pedicels and sometimes the whole pod falls, complete with seeds exposed within; at other times, individual seeds fall to the ground. Many birds search the ground under *Erythrina* trees and shrubs in southern Africa, notably laughing doves (*Stigmatopelia senegalensis*), cape turtle doves (*Streptopelia capicola*) and red-eyed doves (*Streptopelia semitorquata*). Though there may be a plentiful supply of the red seeds of these erythrinas on the ground, the birds do not touch them, while readily picking up wheat or maize grains and other, indigenous, seeds and fruits.

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HOST ASSOCIATIONS OF *SPECULARIUS IMPRESSITHORAX* (PIC) (INSECTA: COLEOPTERA: BRUCHIDAE) WITH SPECIES OF *ERYTHRINA* (FABALES: FABACEAE)[1]

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ABSTRACT

Seeds of species of *Erythrina* are seldom damaged by insects because toxic amino acids and alkaloids are present in the cotyledon. No seed beetles (Bruchidae) are known to attack seeds of *Erythrina* in the New World. The African bruchid, *Specularius impressithorax* (Pic), has been recorded in 7 species of *Erythrina* (including 2 species introduced into South Africa from the Neotropics) in Africa and India. Distribution of *S. impressithorax* and its host species are listed.

The beetle family Bruchidae (seed beetles) is widespread throughout the world, and species are especially numerous in tropical and subtropical regions. Larvae in this family without exception feed in seeds, but adults are pollenophagous, often feeding in flowers of plants other than the larval host plant. Eggs are deposited on the surface of the seed pod, or in some cases on the seed itself, and the newly hatched larva bores through the valve and/or seed wall into the cotyledon. All larval instars are spent in the cavity excavated by feeding activities, and the cavity in most cases is subsequently used as a pupal chamber. Following eclosion, the adult either chews an exit tunnel through the seed coat, or in some cases emerges through a tunnel excavated to the surface by the larva. Exit holes of bruchids are round and cleanly cut whereas those of other insects are ragged and irregular.

The majority of known host associations of bruchids are in the order Fabales. Many bruchids are host specific (a species of bruchid preferring only one host species), but the more prevalent relationship is a species of bruchid being associated with two or more species in a plant genus. Some bruchids are less discriminating and may be associated with species in several plant genera, or even several plant families.

Certain toxic compounds in seeds are effective deterrents to bruchid attack or development. A few legumes are entirely free of bruchid infestation, apparently due to the presence of toxins—e.g., *Gliricidia sepium* (Jacq.) Steud, *Gymnocladus dioica* (L.) Koch, and *Robinia pseudoacacia* L. (Janzen, 1969), but in others, e.g., *Abrus precatorius* L., *Dioclea megacarpa* Rolfe, *Oxytropis* spp., *Astragalus* spp., *Enterolobium cyclocarpum* (Jacq.) Griseb., certain species of *Erythrina*, one or more species of bruchids have either "developed" detoxification sys-

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[1] We wish to thank the following workers for contributions of infested seeds: B. A. Krukoff, N.Y. Botanical Garden; I. Whitton, Durban, South Africa; T. Muller, Salisbury, Rhodesia; and P. H. Raven, Missouri Botanical Garden, St. Louis. We are grateful also to Dr. Krukoff for identifying seeds.

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tems in reaction to the specific toxin in the seed and are able to develop normally, or are in some other way unaffected by the toxin.

Erythrina is a widespread tropical and subtropical genus of 108 species of trees, shrubs, and herbs (Krukoff & Barneby, 1974) and is presently the subject of extensive and intensive studies being reported in this symposium. The seeds of most species in this genus contain relatively high amounts of alkaloids and amino acids which apparently are effective in thwarting attacks of most species of bruchids. No native species of *Erythrina* in the New World is known to be attacked by native bruchids. The report of *Mimosestes amicus* (Horn) found in pods of *Erythrina flabelliformis* Kearney in Arizona (Raven, 1974: 330) is apparently only an instance of the bruchid using the pod as a hibernaculum because it has not been subsequently repeated. The report of *Stator pruininus* (Horn) in *Erythrina* seeds in Hawaii (Bridwell, 1938: 71) is probably a similar situation.

In the Old World, the bruchid, *Specularius impressithorax* (Pic), is known to attack at least seven species of *Erythrina*. Raven (1974: 330) reports one additional species of *Erythrina* exhibiting apparent bruchid damage. Wherever infestations occur, however, they are usually quite heavy, indicating that toxic compounds have little effect in reducing populations of this species. The detoxification mechanism of *S. impressithorax* has not been investigated.

Specularius was described by Bridwell in 1938 for his new species *erythrinae* (p. 71), now a synonym of *impressithorax* (Pic) (Decelle, 1951: 177). The generic name refers to the glabrous, mirrorlike circular area on the pygidium in both sexes. Of the nine species and varieties assigned to this genus, only *impressithorax* (Pic) and *erythraeus* var. *speculifer* (Pic) possess this character. The females of most species of *Gibbobruchus* Pic, a New World genus, are in part also characterized by a speculate pygidium, but the relationships of *Specularius* and *Gibbobruchus* remain to be defined, although they superficially resemble one another. A taxonomic study of *Specularius* and its relationships is needed but is beyond the scope of this paper.

Specularius impressithorax is a small bruchid, 3.25 to 4.25 mm in length, yellowish brown with grayish flecks, and with prominent gibbosities marked with black on the pronotum and on the basal half of the elytra (Figs. 1–2). The antenna is serrate (Fig. 6). The hind femur is enlarged and carries a strong tooth on the inner margin (Fig. 7). The speculate pygidium is easily visible without magnification (Fig. 3). Although the species varies somewhat in size and extent of dark marks on the dorsal surface, we consider this normal variation. Male genitalia as in Figs. 4–5.

The range of the variety *minor* Zacher is widely separated from the principal range of the species and may represent a separate species, but study material is too limited to decide this question. This variety has been reared from *Erythrina senegalensis* A. DC. in Nigera (Zacher, 1952: 467) and Ghana (specimens in British Museum (N.H.), London), from *E. mildbraedii* Harms (reported as *altissima* Aug. Chevalier) in Nigeria (Zacher, 1952: 467) as well as from "*Strophostyles sarmentosa*" (sic) in Guinea Bissau. Without indication of host plants, this variety is also known from Senegal (Museum of Paris), Sierra Leone (British Mu-

Figures 1–3. Morphology of *Specularius impressithorax* (Pic).—1. Dorsal aspect.—2. Lateral aspect.—3. Caudal aspect showing speculate pygidium.

seum), Zaïre (in the central forest region, Museum of Tervuren), and Angola (British Museum).

A short series of specimens reared from *Erythrina mildbraedii* Harms in Nigeria may be still another species, but again study material is limited and no voucher seeds or plants are available.

Other species presently assigned to *Specularius* have been reared from species of *Psophocarpus* and *Rhynchosia*. *Specularius boviei* (Pic) was sampled on *Physostigma mesoponticum* Taub. in Angola, and this plant is likely the host of this bruchid (Decelle, 1975: 18).

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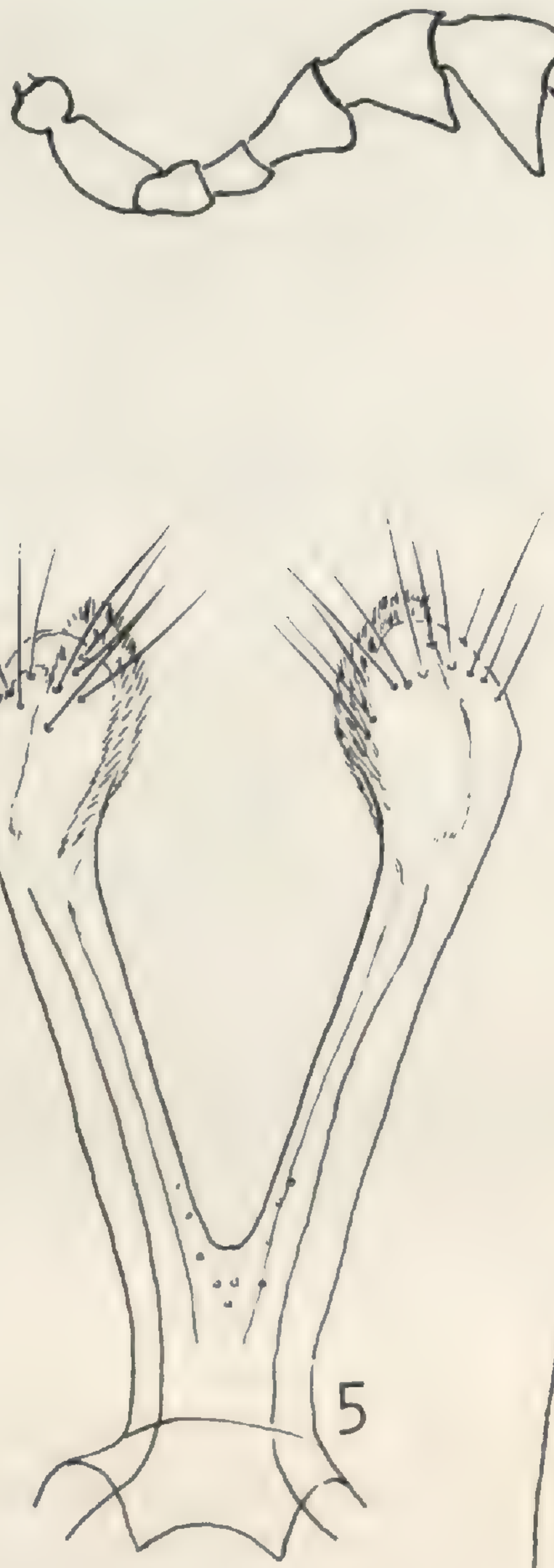

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6

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FIGURES 4–7. Morphology of *Specularius impressithorax* (Pic).—4. Male genitalia, median lobe, ventral aspect.—5. Male genitalia, lateral lobes, ventral aspect.—6. Antenna.—7. Hind leg, lateral aspect.

The nominal form of *Specularius impressithorax* (Pic) was collected in Sudan, Eritrea (Cheran, Museum of Paris), Zaïre (Kivu), Uganda, Kenya, Tanzania, Rhodesia, and South Africa (Transvaal, Natal, East of Cape Province). This form has been introduced into India and Sumatra (Bridwell, 1938: 73–74).

The species of *Erythrina* with which *Specularius impressithorax* has definitely been associated and the countries where these associations have been reported are:

E. abyssinica A. DC. (also reported as *tomentosa* A. Richard): Sudan (holotype of *impressithorax*), Tanzania (Bridwell, 1938: 73), Zaire (Decelle, 1951: 177, 1958: 76), Rhodesia (ex seeds coll. Muller, 1976).

E. caffra Thunberg (also reported as *constantiana* M. Micheli): South Africa (Zacher, 1952: 467; Decelle, 1975: 17; specimens in the British Museum).

E. cristi-galli L.: introduced from South America into Natal (Westville) (ex seeds collected by Whitton, 1976). New host record.

E. humeana Sprengel: South Africa (USNMNH Coll., Washington, D.C.). New host record.

E. latissima E. Meyer: South Africa (ex seeds collected by Whitton, 1976). New host record.

E. pallida Britton & Rose: introduced into Natal, South Africa, probably from the West Indies (ex seeds collected by Whitton, 1976). New host record.

E. variegata L. (also reported as *indica* Lam.): India (Bridwell, 1938: 73; Zacher, 1952: 467); also reared from seeds contributed by Raven and Krukoff.

Raven (1974: 330) reported that seeds of *Erythrina livingstoniana* Baker and *E. milbraedii* Harms exhibited bruchid damage, but we have not seen any beetles from these samples. Samples of seeds of *E. lysistemon* Hutchinson from South Africa and *E. stricta* Roxburgh from India were free of attacked bruchids. Bridwell (1938: 74) lists S. *impressithorax* from Sumatra although no host was listed.

Although New World species of *Erythrina* are not known to host native bruchids, the association of S. *impressithorax* with the two species of *Erythrina*, *pallida* and *crista-galli*, introduced into South Africa, strongly suggests that the method of circumventing the toxins in *Erythrina* by *impressithorax* may be effective for many of the New World *Erythrina*, but that the opportunity for infestation is lacking. Future research should include controlled attempts at infesting seeds of non-African species of *Erythrina* by *impressithorax*.

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STUDIES OF *ERYTHRINA* ALKALOIDS, PART III.[1] G.C./M.S. INVESTIGATIONS OF ALKALOIDS IN THE SEEDS OF A FURTHER FOURTEEN SPECIES[2]

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Abstract

Fourteen species of *Erythrina* were characterized for the total alkaloids content, both in the free form and as glycosides, by gas chromatography-mass spectrometry. Thirteen alkaloids were identified in all, the most common being erysodine, erysovine, and erysopine. A number of unknown or unidentified were also noted.

In two previous papers (Games et al., 1974; Barakat et al., 1977) we described preliminary studies of the occurrence of alkaloids in the seeds of some 26 species of *Erythrina*. In the present work we have continued using gas chromatography-mass spectrometry (g.c./m.s.) to analyze the alkaloid content of 14 further species, and as in the earlier studies (Barakat et al., 1977), we have characterized the total alkaloids occurring both in the "free" form and as their glycosides; the latter were hydrolyzed to enable the "liberated" alkaloids to be analyzed. Hydroxyl groups were derivatized as their trimethylsilyl (TMS) derivatives before g.c./m.s., and the individual alkaloids present in each species were characterized by comparisons of their mass spectra with those of authentic materials isolated from other species, and with data reported in the literature. A number of new alkaloids were also detected in the course of this work, but full characterization will depend on the availability of sufficient seeds for preparative isolation of the alkaloids concerned.

Alkaloids in *Erythrina* Species

The results of the present studies with the seeds of 14 species are shown in Table 1, and for comparison earlier findings by other workers with nine of these species are recorded in Table 2. The previous work depended largely on classical separation methods, i.e., crystallization and column chromatography, the one exception being Rinehart's investigations (Hargreaves et al., 1974) of *Erythrina flabelliformis* seeds, which like our own work involved g.c./m.s. As indicated in the list of sources of seeds used in our studies, several diferent samples of seeds collected at different times (some were more than 30 years old), or in different

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[1] Our previous two papers (Games et al., 1974; Barakat et al., 1977) are regarded as parts I and II.

[2] We are very grateful to B. A. Krukoff for supplying all the seeds used in this work, and for his keen interest in the results. We are also pleased to record our gratitude for a grant towards this work from the F. B. and B. A. Krukoff Memorial Fund, and we thank the S.R.C. for assistance in the purchase of the mass spectrometer used in this work. We thank Mr. M. Rossiter for assistance in running the mass spectra.

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TABLE 1. Occurrence of alkaloids in 14 species of *Erythrina* seeds examined in Cardiff.

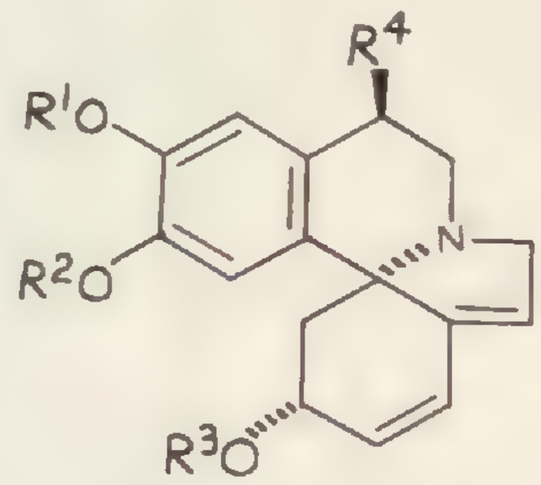
Species of Seeds	No. of Samples	Dienoid							Alkenoid							
		Erysotrine (1)	Erysodine (3)	Erysovine (4)	Erythravine (5)	Erysopine (7)	Erysonine (8)	Erysoline (9)	Erythratidine (11)	Erysotine (13)	Erysosalvine (14)	α-Erythroidine (17)	β-Erythroidine (18)	Erybidine (20)	No. of Unknown/ Unidentified Alkaloids
2. *E. crista-galli*	2	+	+	++		++			++					+[a]	3
3. *E. falcata*	1		+	+		+	+	+							2
4. *E. dominguezii*	1		+	+		+	+	+	+	+	+				1
6. *E. verna*	4		++	++		+	+	+	+++	+	+				2
8. *E. suberosa*	1		+++	+		+									3
14. *E. breviflora*	2		+	+	+	+				+					1
22. *E. herbacea*	4		++	++		+			++[b]	+[b]					3
24. *E. flabelliformis*	6		+	+		+		+							2
51. *E. americana*	1			+		+						+++	+++		1
58. *E. amazonica*	1		+	+		+									3
62. S. *pallida*	1		+	+		+									3
87. *E. addisoniae*	1		+	+		+	+						+		1
90. *E. sacleuxii*	1		+	+		+	+								1
101. *E. velutina*	3		+	+		+	+		+						2

[a] Erybidine only found in sample (a).
[b] Erythratidine and erysotine were only found in sample (b).

TABLE 2. Occurrence of alkaloids in *Erythrina* species determined in other laboratories.

Species and Parts	Dienoid						Alkenoid											References
	Erysotrine (1)	Erythraline (2)	Erysodine (3)	Erysovine (4)	Erythrinine (6)	Erysopine (7)	Erythramine (10)	Erythratidine (11)	Erythratine (12)	Erythratinone (15)	Christamidine (19)	α-Erythroidine (17)	β-Erythroidine (18)	Erybidine (20)	Hypaphorine (22)	N-nororientaline (21)	Erysotramidine (16)	
2. *E. crista-galli*																		
seeds	+	+	+	+		+	+	+							+			Folkers et al., 1941; Deulofeu et al., 1947
leaves	+	+	+		+											+	+	Ito et al., 1973, 1976
heart wood, bark, roots	+	+			+			+	+	+	+			+		+		Barton et al., 1968; Ito et al., 1973, 1976
3. *E. falcata* seeds			+	+		+												Gentile & Labriola, 1942; Deulofeu, 1952
4. *E. dominguezii* seeds			+	+		+									+			Folkers et al., 1941; Gentile & Labriola, 1942
8. *E. suberosa* seeds, leaves	+		+												+			Singh & Chawla, 1969, 1970; Miana et al., 1972
22. *E. herbacea* seeds			+			+												Folkers & Koniuszy, 1940a
24. *E. flabelliformis* seeds			+	+		+												Folkers & Koniuszy, 1940b
seeds	+		+	+														Hargreaves et al., 1974
51. *E. americana* seeds			+	+								+	+					Folkers & Major, 1937; Folkers & Koniuszy, 1940b
62. *E. pallida* seeds			+	+		+												Folkers & Shavel, 1942; Folkers et al., 1944
101. *E. velutina* seeds		+	+	+														Folkers & Koniuszy, 1940a; Folkers & Shavel, 1942

TABLE 3. Structures of dienoid alkaloids.

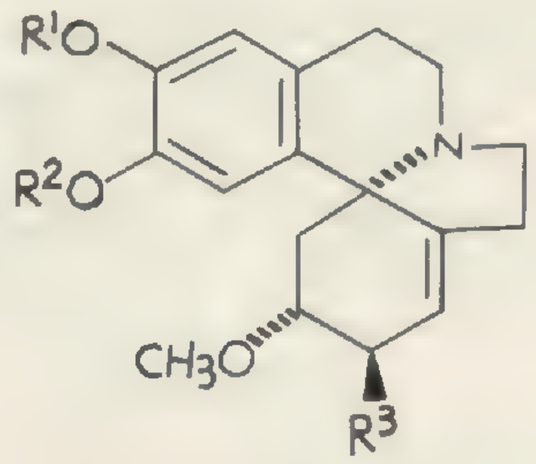


	R¹	R²	R³	R⁴
(1) Erysotrine	CH_3	CH_3	CH_3	H
(2) Erythraline	–CH_3–		CH_3	H
(3) Erysodine	H	CH_3	CH_3	H
(4) Erysovine	CH_3	H	CH_3	H
(5) Erythravine	CH_3	CH_3	H	H
(6) Erythrinine	–CH_3–		CH_3	OH
(7) Erysopine	H	H	CH_3	H
(8) Erysonine	H	CH_3	H	H
(9) Erysoline	CH_3	H	H	H

places, were available with some of the species. Small variations between the alkaloid content of different samples of the same seeds are also noted in Table 1, and there are also minor differences between our findings and those of earlier workers shown in Table 2. The structures of the various alkaloids are shown in Tables 3, 4 and 5.

The most common alkaloids, and also usually present in greatest abundance in all the species investigated, were erysodine (3) (numbers in parenthesis refer to the compounds listed in Tables 1–5), erysovine (4) and erysopine (7). However, in accord with earlier work (Folkers & Koniuszy, 1940b; Folkers & Major, 1937), the most abundant alkaloids (>90%) in *Erythrina americana* were α- and β-erythroidines (17) and (18), although small amounts of erysodine, erysovine and erysopine were also detected. Our results also showed that erysonine (8), erysoline (9), erythratidine (11) and erysotine (13) occurred in about half the species studied. Erysosalvine (14) was only found in two species, *E. dominguezii* and *E. verna*, whilst erythravine (5) and erybidine (20) were each only found in one species (*E. breviflora* and *E. crista-galli* respectively). Although several alkaloids were found in *E. addisoniae*, these included only one of the erythroidine isomers (18), whereas in other species containing erythroidines both isomers are normally present (cf. Games et al., 1974; Barakat et al., 1977; Hargreaves et al., 1974), although the proportions may vary. As in the earlier studies, the isomeric alkaloids erysonine (8) and erysoline (9) could not be distinguished from each other by mass spectrometry, but their TMS derivatives had slightly different retention times on gas chromatography, that of erysonine (8) being eluted first.

TABLE 4. Structures of alkenoid alkaloids.



	R¹	R²	R³
(10) Erythramine	–CH₂–		H
(11) Erythratidine	CH_3	CH_3	OH
(12) Erythratine	–CH₂–		OH
(13) Erysotine	H	CH_3	OH
(14) Erysosalvine	CH_3	H	OH
(15) Erythratinone	–CH₂–		=O

A number of unknown alkaloids (as specified in Table 1) were also detected in each species, mostly in rather smaller amounts than the three most abundant alkaloids. Mass spectral evidence, based on the trimethylsilyl derivatives, indicated that some of these unknown alkaloids contained one, or more, hydroxyl groups; in the case of *Erythrina suberosa* preliminary indications of the presence of 11-hydroxy and 11-methoxy alkaloids were also obtained.

It is interesting to note from Table 2 that since our original report indicating that 11-oxygenated alkaloids might be largely confined to Old-World species of *Erythrina*, Japanese workers (Ito et al., 1973) have described the occurrence of erythrinine (6) in *E. crista-galli*. However, their studies were carried out with plants cultivated in Japan, doubtless one of the numerous cultivated forms of this species. We failed to detect erythrinine in wild plants of American origin.

Further work on the isolation and characterization of both the known and unknown alkaloids in each species is in progress (where sufficient seeds are available) using high pressure liquid chromatography.

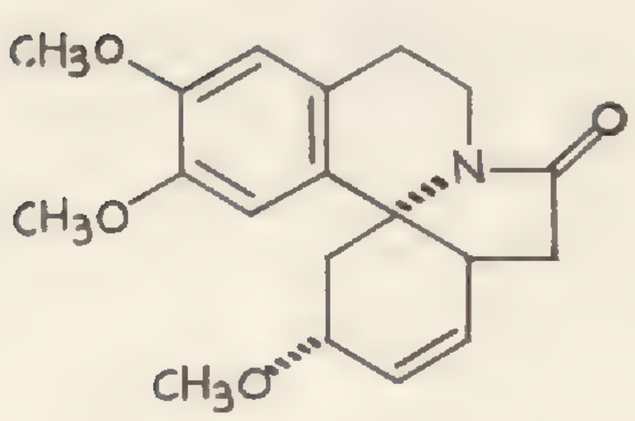
SOURCES OF *ERYTHRINA* SEEDS

All the seeds used in these studies were supplied by B. A. Krukoff and most are backed by herbarium material deposited at the New York Botanical Garden and other herbaria.

2. *E. crista-galli* L.; (a) Meyer s.n./1974—California.
   (b) Krukoff Herb. 9187[5]—Argentina.

[5] Seed samples marked "Krukoff Herb." are very old, having been collected in the early 1940s in connection with studies of alkaloids in the genus by K. Folkers and others.

TABLE 5. Structures of other alkaloids.



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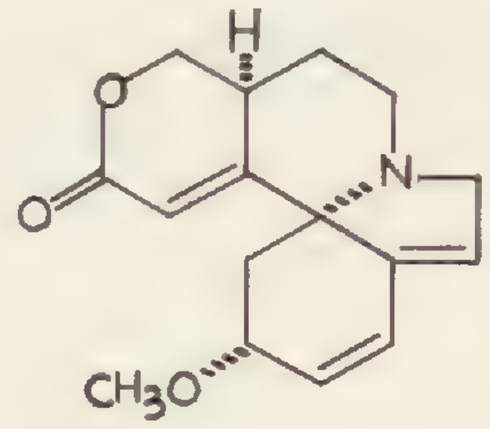

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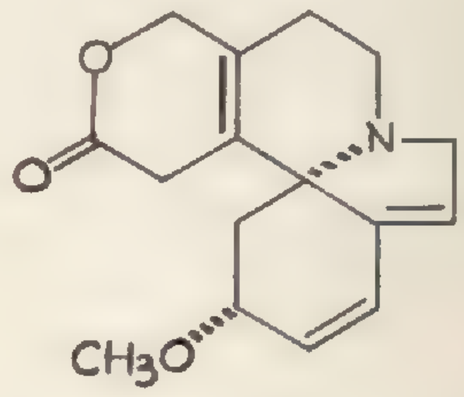
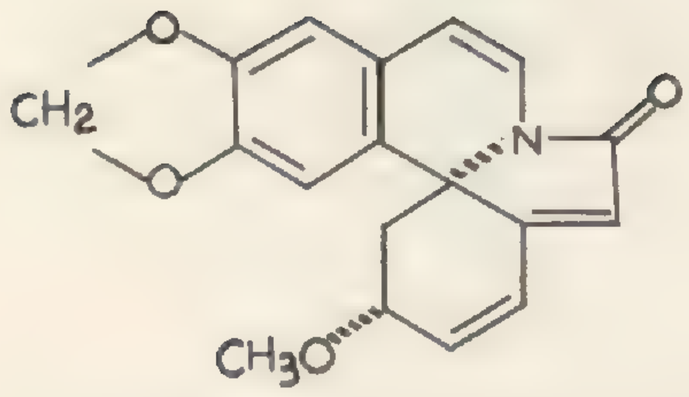


(18)



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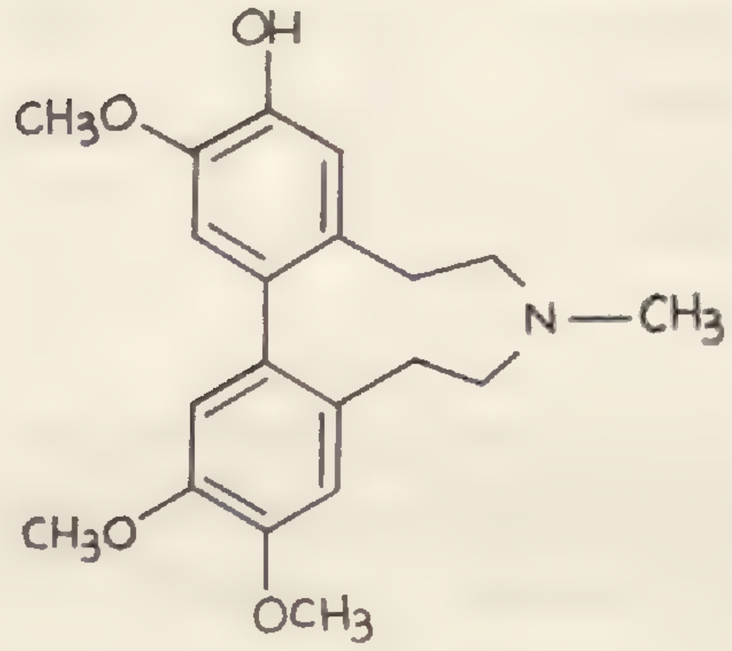

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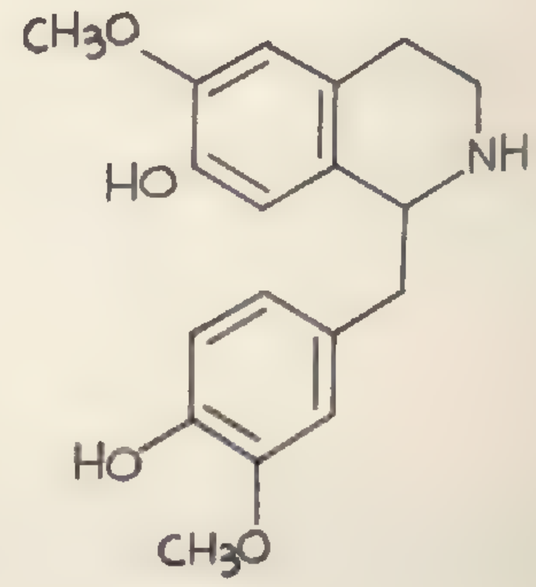

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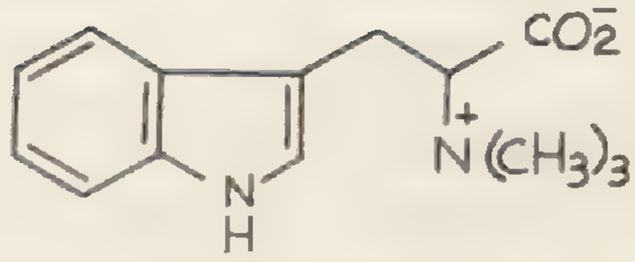

(22)

3. *E. falcata* Bentham; Krukoff Herb. 15396—Buenos Aires, Argentina.
4. *E. dominguezii* Hassler; Krukoff Herb. 15378—Chaco, Argentina.
6. *E. verna* Velloso; (a) Krukoff Herb. 16347—Argentina.
   (b) Krukoff Herb. 17732—Brazil.
   (c) Krukoff Herb. 16352—Brazil.
   (d) Krukoff Herb. 16665—Brazil.
8. *E. suberosa* Roxburgh; Krukoff Herb. 9864—India.
14. *E. breviflora* A. DC.; (a) Krukoff Herb. 15346—Mexico.

(b) Krukoff Herb. 15379—Mexico.
22a. *E. herbacea* L. subsp. *herbacea*; (a) Krukoff Herb. 16627—Louisiana, U.S.A.
(b) Krukoff Herb. 15578—Texas, U.S.A.
(c) Krukoff Herb. 18883—Florida, U.S.A.
(d) Clifton s.n./1978—Florida, U.S.A.
24. *E. flagelliformis* Kearney; (a) Sally's seeder s.n./1975—Arizona, U.S.A. (5 samples).
(b) Lyle Angus McGill—Arizona, U.S.A.
52. *E. americana* Miller; Krukoff Herb. 16881—Veracruz, Mexico.
59. *E. amazonica* Krukoff; Krukoff Herb. 9515—Maranhão, Brazil.
63. *E. pallida* Britton & Rose; Krukoff Herb. 15183—Trinidad.
88. *E. addisoniae* Hutchinson & Dalziel; A.A. Enti s.n./1978—Kumasi, Ghana.
91. *E. sacleuxii* Hua; Faden 74/294—Kenya.
102. *E. velutina* Willd.; (a) Dardano Lima s.n./1974—Brazil.
(b) Dardano de Andrade s.n./1974—Brazil.
102a. *E. velutina* forma *aurantica* (Krukoff) Ridley; Lima s.n./1974—Brazil.

Experimental Methods

The alkaloids were isolated from the seeds by similar methods to those used previously (Games et al., 1974; Barakat et al., 1977; Deulofeu et al., 1947), and the mass spectra were determined with a Varian CH 5D mass spectrometer coupled with a Varian 1740 gas chromatograph via a two stage Watson-Biemann separator. The temperature of the ion source was 220°C and the accelerating and ionising potentials were 3 Kv and 70 eV respectively. Spectra were recorded electrically using a Varian 620i data system, and after subtraction of background peaks were normalized and plotted on a Statos 21 fast printer. Field ionization and desorption mass spectrometry were used for preliminary studies of the crude alkaloid mixtures before chromatography.

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NOTES ON PROPAGATION AND CULTIVATION OF *ERYTHRINA* IN HAWAII[1]

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ABSTRACT

Successful methods of propagation from seeds and by cuttings for *Erythrina* species are described. Species cultivated in the Waimea Arboretum, Haleiwa, Hawaii are listed, and information on their flowering periods is given.

Erythrina may be propagated easily from seeds, by cuttings or air layers, and probably also by grafting. In Hawaii, propagation from seeds and by cuttings are the most commonly used techniques.

PROPAGATION FROM SEEDS

Fresh seeds and those harvested within 3–6 months of maturity can be sown without any special treatment. Germination rates are generally high and are often 100%. Seeds over 6 months old may take between 12 and 18 months to germinate due to their hard seed coat which becomes tougher with age. They need to be specially treated by one of the following methods to hasten and improve germination. They may be dropped into water which has just fallen below boiling point and left in the water as it cools for a minimum of one hour. If the seeds are three years old or more, they should be left to soak in the water for 10 to 12 hours and then sown in the usual way. As this method can kill the embryo if the seed coat is not very hard, it is preferable to file the seeds with a slender triangular file. A groove can be made through the sides of the seed coat with care so as to avoid damaging the cotyledons or embryo, which usually results in the death of the seeds from fungal attack or in malformed and weakened seedlings.

Seeds of most species produce strong seedlings from healthy seeds in almost any well-drained soil, with a minimum of trouble from damping-off disease. However, as it is difficult to obtain seeds of many of the rarer species, it is wise to use a partially sterilized soil and to add sand and peat. Some gravel, or cinder as is used in Hawaii, ensure drainage and rapid root growth. Air movement around the seedlings is beneficial.

A similar soil mixture, without sterilized soil, can be used for potting. The first potting of seedlings can be carried out when they are 5–8 cm high. Shade is essential for their survival during the first few days. Species successfully germinated are indicated in Table 1.

PROPAGATION BY CUTTINGS

Propagation by cuttings can be rapid and successful depending on the species used, the time of propagation, and the maturity of the wood. At Waimea Ar-

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TABLE 1. Records of germination of seeds and/or propagation by cuttings of *Erythrina* at Waimea Arboretum, Haleiwa, Hawaii.[a]

(1) FROM SEEDS

Name[b]	Collector	Date Sown & Quantity[c]	First Germination	Final Germination & Date Potted
13. *E. subumbrans* (74s1766)	From Matrimandir Gardens (India)	10/31/74 (6-H.W.)	1/1/75 (1 Germ.)	----------
36. *E. chiapasana* (74s861)	Krukoff 1973/16 (Guatemala)	6/21/74 (21-H.W.)	6/30/74 (3 Germ.)	7/8/74 (5 potted)
43. *E. guatemalensis* (74s874)	From same tree as Krukoff 1974/2 (Guatemala)	6/20/74 (5-H.W.)	7/8/74 (1 Germ.)	8/2/74 (1 potted)
49. *E. lanceolata* (75s2134)	Antonio Molina 1975/s.n. (Honduras)	11/3/75 (5-filed)	11/25/75 (5 Germ.)	11/25/75 (5 potted)
53. *E. berteroana* (74s864)	From same tree as Krukoff 1968/508 (Guatemala)	6/21/74 (36-H.W.)	7/11/74 (8 Germ.)	7/15/74 (11 potted)
59. *E. amazonica* (76s449)	N. T. Silva 4238 (Brazil)	4/15/76 (5-H.W.)	6/8/76 (1 Germ.)	6/21/76 (2 potted)
70. *E. oliviae* (77s330)	Joel Mejicanos 1977/1 (Mexico) (from same tree as type)	4/23/77 (13-filed)	5/5/77 (1 Germ.)	5/13/77 (12 potted)
85. *E. decora* (76s946)	W. Giess 1976/s.n. (S. West Africa)	10/27/76 (4-filed)	11/4/76 (1 Germ.)	11/17/76 (2 potted)
		10/27/76 (no treatment)	11/4/76 (1 Germ.)	11/17/76 (2 potted)
105. *E. burana* (74s884)	A. Getahum 1974/s.n. (Ethiopia)	6/20/74 (5-H.W.)	7/11/74 (1 Germ.)	7/23/74 (5 potted)

(2) FROM CUTTINGS

Name	Collector	Date Inserted	Date & Number Potted
26. *E.* aff. *coralloides* (74c1451)	Krukoff 1970/133 (Mexico)	9/20/74 (2-to mist) Rootone 'F' used	3/19/75 (2 potted)
38. *E. cobanensis* (74c1453)	From same tree as Krukoff 1969/195 (Guatemala)	9/20/74 (3-to mist)	10/16/74 (1 potted)
		10/25/74 (1-to mist) both rec'd. Rootone 'F'	7/2/75 (1 potted)
40. *E. tajumulcensis* (74c1448)	From same tree as Krukoff 1969/249 (Guatemala)	9/20/74 (4-to mist)	Died
		10/16/74 (4-to mist) both rec'd. Rootone 'F'	10/16/74 (4 potted)
43. *E. guatemalensis* (74s874)	Krukoff 1974/2 (Guatemala)	12/10/74 (2-to mist) Rootone 'F' used	6/2/75 (1 potted)

[a] All propagated material used in this experiment was originally received as seeds and identified by B. A. Krukoff (except for *E. subumbrans*).
[b] Waimea Arboretum accession numbers follow the names.
[c] H.W.—stands for Hot Water Treatment, and the preceding number stands for the number of seeds or cuttings used.

boretum we have had the poorest results from soft tips, and short, soft, side-shoots under mist propagation. However, terminal or side-shoots from mature wood usually give satisfactory results under intermittent mist or in a shaded propagating bed where they are misted manually two or three times a day.

The best medium is coarse sand or one with a high proportion of coarse sand. The addition of other materials has shown little benefit, and an abundance of peat or vermiculite has given poor results. Some workers have reported good results with pure perlite, but we have not found this to be so. The roots of plants from a sand medium tend to be tough and to suffer less during transplanting.

The best wood to use is fully matured, firm branch ends or short side growths, 20–25 cm long. We have had excellent results with these when they have been taken at the end of the growing season or just as the new growth begins in the spring.

We have found that any well-drained mixture can be used for potting, and that the application of a slow release fertilizer a few weeks after potting is beneficial. It is important to keep the roots from becoming pot-bound by repotting when necessary. Some species are partricularly adverse to crowded root conditions and take a long time to establish a strong root system after they are planted out. Plants which are about 6 dm high from 1 gallon pots will grow well in the ground and there is no advantage in using larger containers. During the growing season the plants need plenty of water and can be fed at regular intervals with any balanced fertilizer. Species successfully propagated by cuttings are indicated in Table 1.

Cultivated Species in Hawaii

An extensive collection of *Erythrina* species has now been established in cultivation at Waimea Arboretum, Haleiwa, Hawaii. As of October, 1978, 71 species and 1 named hybrid had been successfully established. The following 23 species have been identified by B. A. Krukoff after having flowered at Waimea:

1. *E. fusca* Loureiro
2. *E. crista-galli* L.
4. *E. dominguezii* Hassler
13. *E. subumbrans* (Hasskarl) Merrill
16. *E. speciosa* Andrews
22a. *E. herbacea* L. subsp. *herbacea*
26. *E.* aff. *coralloides* A. DC.
36. *E. chiapasana* Krukoff
37. *E. atitlanensis* Krukoff & Barneby
40. *E. tajumulcensis* Krukoff & Barneby
42. *E. macrophylla* A. DC.
43. *E. guatemalensis* Krukoff
49. *E. lanceolata* Standley
50. *E. costaricensis* M. Micheli
53. *E. berteroana* Urban
54. *E. rubrinervia* H.B.K.
56. *E. salviiflora* Krukoff & Barneby
59. *E. amazonica* Krukoff
72. *E. lysistemon* Hutchinson
73. *E. humeana* Sprengel
94. *E. latissima* E. Meyer
96. *E. variegata* L.
97. *E. tahitensis* Nadeau

An additional 40 named species, one named hybrid and 8 unidentified erythrinas remain to be identified and/or their names checked once they will be in flower.

Initial observations of the flowering periods of some *Erythrina* species have now been made and are presented in Table 2.

TABLE 2. Observations on flowering periods[a] of some *Erythrina* species at Waimea.[b]

1. *E. fusca* Loureiro (74s99)	Feb. 1977; Mar. 1977.
1. *E. fusca* Loureiro (74s1768)*	Feb. 1977.
2. *E. crista-galli* L. (74p840)	Apr. 1977; May 1978.
13. *E. subumbrans* (Hasskarl.) Merrill (74s1766)	Feb. 1977; Jan.–Feb. 1978.
16. *E. speciosa* Andrews (74s853)	Dec. 1976; Dec. 1977.
16. *E. speciosa* Andrews (74s856)	Dec. 1976; Jan. 1977; Jan.–Feb. 1978.
22A. *E. herbacea* L. subsp. *herbacea* (75c1103)	Dec. 1976; Jan.–Mar. 1977; Apr.–May 1978.
22A. *E. herbacea* L. subsp. *herbacea* (76s187)*	Dec. 1976; Mar. 1977.
26. *E.* aff. *coralloides* A. DC. (74c1451)	May 1978.
36. *E. chiapasana* Krukoff (74s861)	Mar. 1977; Feb.–Mar. 1978.
37. *E. atitlanensis* Krukoff & Barneby (74s98)	Feb. 1978.
40. *E. tajumulcensis* Krukoff & Barneby (74c144)	Apr.–May 1978.
42. *E. macrophylla* A. DC. (74s97)	Dec. 1977.
42. *E. macrophylla* A. DC. (74s858)	Feb.–May 1978.
43. *E. guatemalensis* Krukoff (74s103)	Mar. 1977; Apr.–May 1978.
50. *E. costaricensis* M. Micheli (74c1450)	Jan.–Feb. 1978.
52. *E. americana* Miller (76c261)*	Feb. 1978.
53. *E. berteroana* Urban (74s854)	Feb. 1978.
53. *E. berteroana* Urban (74s862)	Apr.–May 1978.
53. *E. berteroana* Urban (74s864)	Mar. 1977; Apr.–May 1978.
54. *E. rubrinervia* H.B.K. (74p325)	Jan.–May 1978.
56. *E. salviiflora* Krukoff & Barneby (74s859)	Apr.–May 1978.
96. *E. variegata* L. (74s877)—"boninensis"—	Jan.–Feb. 1977; Jan.–Mar. 1978.
96. *E. variegata* L. (74s1249)—collected in Guam	Feb. 1978.
96. *E. variegata* L. (75c1173)—"phlebocarpa"—	Feb. 1978.
96. *E. variegata* L. (76c183)	Apr.–May 1978.

[a] The flowering period noted is not necessarily the *total* period of flowering in a given year. It is a record of actually noted flowering.

[b] The identifications of the above plants were checked by B. A. Krukoff with the exception of the three marked with asterisks.

FURTHER NOTES ON RETZIACEAE: ITS CHEMICAL CONTENTS AND AFFINITIES

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ABSTRACT

Retziaceae is a taxonomically isolated monotypic family of the Cape Region of South Africa. It has been related in the past to Convolvulaceae, Solanaceae, and most recently to Loganiaceae (Gentianiflorae), especially Buddlejeae. The iridoid compounds of Retziaceae, identified here, are distinctive and suggest that the family is unrelated to Gentianiflorae, but is probably allied to Lamiiflorae, including Verbenaceae, Scrophulariaceae, and the endemic Cape family Stilbaceae. There is a remarkable similarity between the iridoids of *Stilbe ericoides* and Retziaceae. A detailed review of morphology, anatomy, biology, and other characteristics of Retziaceae is presented. The suggestion of a relationship between Retziaceae and Stilbaceae appears to find considerable support from morphological as well as chemical considerations.

Retziaceae is a monotypic family consisting of *Retzia capensis* Thunb. This is a conspicuous member of the Cape fynbos or Cape macchia flora in South Africa, where it has a restricted distribution. Its isolated systematic position is undoubted and various efforts have been made to place it taxonomically and to clarify its most likely affinity. Recently evidence was presented on its pollen morphology and chromosome number by Goldblatt & Keating (1976). Further information is given here on its morphology, anatomy, and especially its iridoid glucosides.

THE HISTORY OF *RETZIA* IN LITERATURE

The literature concerning *Retzia* has been surveyed extensively by several workers including Marloth (1932: 540), Leeuwenberg (1964), and Goldblatt & Keating (1976). A review is given below.

Retzia was described by Thunberg in 1776 and named in honor of Anders Jahan Retzius (1742–1821), Botanical Demonstrator and Professor in Natural History in Lund, colleague and contemporary of Thunberg. Among Retzius's botanical contributions should be mentioned *Observationes Botanicae* and *Florae Scandinaviae Prodromus*. His herbarium in Lund contains many duplicates of Thunberg's South African collections.

The family Retziaceae was first described, in a somewhat ambiguous way, by Bartling (1830: 192) as "genera desciscentia (Retzionaceae)" under Convolvulaceae. *Retzia* was accompanied by *Lonchostoma* (now in Bruniaceae), with

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which it was often associated during the following decades. *Retzia* was also placed in Convolvulaceae by Harvey (1838) in his *Genera of South African Flowering Plants*. Retziaceae was regarded as a distinct family next to Apocynaceae by Lindley (1836), and by Agardh (1858), while Endlicher (1836) included *Retzia* in Solanaceae, as did de Candolle (1852). Bentham & Hooker (1876) found an acceptable position for *Retzia* in Solanaceae-Cestreae, within which some taxa undoubtedly resemble *Retzia* superficially, except that they do not have verticillate leaves. This solanaceous affinity gained some support, and *Retzia* continuously appeared in this family in the works of Wettstein (1895), Wright (1904), and Phillips (1926). Retziaceae was still retained in Solanales by Hutchinson as late as 1973.

Fedde (1896) in an anatomical analysis of Solanaceae found *Retzia* to be aberrant in lacking intraxylary phloem, and Solereder (1899) came to the same conclusion. On this evidence Fedde referred *Retzia* to Loganiaceae-Buddlejoideae, and since then several botanists have been inclined to accept a loganiaceous affinity. The fact that Buddlejaceae, like *Retzia*, lacks intraxylary phloem seems to have encouraged this idea, but the placing of *Buddleja* in Loganiaceae has been challenged, for example by Takhtajan (1969), who placed the families Buddlejaceae and Retziaceae in his Scrophulariales, an alternative which gains some support from the data presented here. Leeuwenberg (1964) in his treatment of Loganiaceae distinguishes Buddlejeae and Retzieae as tribes.

Airy Shaw (1973) is representative in expressing great doubts on the affinity of *Retzia*; he places the genus in a separate family with the remark that it is isolated and possibly has connections with Solanaceae, Scrophulariaceae, or families of the order Loganiales, differing from all the latter except Buddlejaceae in the absence of intraxylary phloem.

More recently, Thorne (1976) has placed *Retzia* in a separate subfamily of Loganiaceae, and Buddlejaceae as a separate and adjacent family. Dahlgren (1975) treated Retziaceae and Buddlejaceae as separate families next to Loganiaceae, but admits an alternative position of Buddlejaceae in Scrophulariales with due consideration to the absence of internal phloem and the presence of different (non-seco) types of iridoids. At that time the iridoids in *Retzia* had not been analyzed in detail, though their presence had been confirmed (Jensen et al., 1975). Goldblatt & Keating (1976) in a study of chromosome cytology and pollen microstructure found no evidence for removing Retziaceae from the vicinity of Loganiaceae, although they did not consider the relationship to be close or that it was possible to relate *Retzia* to any particular group in that family.

New evidence presented here suggests an affinity between *Retzia* and the genera of Stilbaceae, the latter often treated as a tribe, Stilbeae, or as a subfamily, Stilboideae, of the Verbenaceae. This alternative, to our knowledge, was first suggested in Dyer (1975), where it was mentioned that "there seems to be some affinity between *Retzia* and the family Stilbaceae which deserves investigation."

The arguments for this possible affinity and the problems involved in the taxonomic groupings will be further discussed below.

FIGURE 1. *Retzia capensis* Thunb.—*Raven & Raven 26127* from slopes near Betty's Bay, Caledon District, South Africa, 1973.—A. Flowering branch.—B. Section of branch with whorls of 4 leaves.—C. Floral bract.—D. Flower with the 2 bracteoles.—E. Longitudinal section of a flower.—F. Upper part of corolla tube with stamens.—G. Ovary with the surrounding thin disc.—H. Transection of an ovary seen from above.—I–J. Capsules, showing septicidal as well as loculicidal dehiscence.—K. Seed.—Del. Bent Johnsen.

MORPHOLOGY (FIG. 1)

Retzia capensis is a sparingly branched shrub, generally 60–130 cm tall with stiff, coarse and strong branches, which are densely villous or at least tomentose on the young parts. There seems to be great variation in length and density of pubescence.

The shrub branches monopodially (like a juvenile, little-branched pine, which it also resembles). This is explained by the fact that the inflorescences are not terminal but borne on strongly suppressed lateral short-shoots. The young branches bear prominent longitudinal ridges, each terminating at a leaf base. On the older parts of the branches the leaf scars appear as more or less distinct spots.

The leaves are usually situated in verticels of 3, 4 or 5; 3 mainly on the thin branches, 4–5 on the main, coarse branches. The leaves are exstipulate, simple, sessile, entire, and linear. They are broadest near the base tapering towards the obtuse or subacute apex. Their size varies from less than 30 × 3 mm up to more than 50 × 6 mm; they are small on the thin lateral branches but large in the floriferous region, especially on the short shoots. The leaves are often subglabrous, puberulous mostly on the basal parts and closely so on the basal margins, but the large leaves in the inflorescence region, i.e., mostly on the lateral short-shoots, may be pubescent on most parts except the apices and are densely white-pubescent along the margins. Actually, the young leaves are hairy, but the hairs are shed later to make the leaves glabrescent.

The leaves are "ericoid" in appearance in the sense that the margins are strongly revolute in the apical parts, where the margins enclose a narrow furrow or canal on each side; these continue as longitudinal grooves all along the lower side of the leaf at some distance from the margins, which are not revolute on the middle and basal parts of the leaves. These grooves often carry some short pubescence. In periods of extreme dryness of the air, according to Marloth (1932), the leaves shrink, and their margins are forced closer against the midrib, this converting the grooves into tubes, which is the normal condition at the apex. The leaf base is tightly pressed against the branch.

The flowers are crowded on short-shoots concentrated at the distal part of the branches, but often not at the branch tips, which grow continuously. On the floriferous part, very contracted short-shoots are borne in the leaf axils. These short-shoots are multifoliate and each represents a compact spike of a few, closely set flowers, the lowest often suppressed in their leaf axils.

Generally only 1 or 2 flowers develop fully at a time on each short-shoot. Though the flowers are densely clustered, they seem to be arranged in decussate pairs, each one in the axil of a large, hairy leaf and supplied on the very (ca. 1 mm) short, white pubescent pedicel with 2 bracteoles. These are similar to but smaller than the leaves: linear, puberulous, varying in size between the flowers but frequently reaching about as far as the calyx lobes. (This "compound" nature of the inflorescence region rarely seems to have been understood by previous investigators.)

The flowers are most conspicuous. The calyx is tubular and slightly tapering at the base; the tube is pale, ca. 10–13 mm long, glabrous towards the base, puberulous in the middle and distal parts; and the lobes are linear-lanceolate, ca. 8–12 mm long, pointed, puberulous to short-sericeous but with denser and longer white hairs on the margins.

The corolla is tubular, ca. 6–7 mm wide, and 55–65 mm long including the 5 triangular-ovate, ca. 8–11 mm long lobes, which have a valvate to reduplicate-

valvate aestivation. While the corolla tube is brightly red to orange red, the lobes are dark, (bluish) black, though the color on the tips of the lobes is masked by long white pubescence. The corolla tube is diffusely ribbed from the sinuses (where the stamens are inserted) and puberulous on the outer side, becoming subglabrous towards the base.

There are always 5 stamens developed in *Retzia*. The filaments, inserted in the sinuses between the corolla lobes, are 4–5 mm in length, and the dorsifixed, versatile, introrse anthers are ca. 2.5–3 mm long. The 2 thecae of each anther are fused in the upper half but free from each other in the lower half and often more or less distant at the base. They are obtuse at both ends (the anthers are not sagittate as sometimes stated).

An annular, undulating disc encircles the base of the ovary. The pistil is bicarpellate. It has a long, very slender, glabrous style reaching out of the corolla tube and greatly exceeding this at early anthesis, pointing up to 10 mm or more out of the yet mostly closed corolla. The style apex is shortly bilobate, with stigmatic papillae on the inner side of the lobes. The ovary is incompletely bilocular. There is a complete basal septum reaching to about a third of the ovary height, while in the upper part of the ovary there is free connection between the locules and merely along each carpel margin a rib projecting towards but not fused in the middle. The 2 placentae are situated at the top of the septum center; each bears 1 or 2 closely situated pendulous ovules and 1 ascending; thus there are usually 4–6 ovules in the ovary. (Some of the ovules in a collection studied were transformed into a long, winding, threadlike strand growing towards the base of the stylar canal.)

The fruit is a longitudinally dehiscent capsule, the construction of which is not always correctly understood. It is often strongly folded (Figs. 1I–1J) but has a smooth surface. When well matured it is 7–9 mm long, but sometimes it is considerably smaller. The dehiscence starts *loculicidally* at the apex and proceeds downwards to about a third of the length; each valve apex often becomes bilobate or cleft as it often breaks up septicidally by a longitudinal fissure along each suture. The capsule is enclosed in the long-persistent perianth and enveloped by the leaves of the short shoots.

The seeds are up to 6 mm long, elongate-triangular and somewhat crested, strongly reticulate from the thickened lateral and inner walls of the epidermis cells of the testa. The embryo is surrounded by mealy endosperm; it is straight, cylindric and almost as long as the endosperm (Leeuwenberg, 1964).

Anatomy

The anatomy is described in detail in a still unpublished thesis by Herbst (1972) and therefore has not been included in this study. A few observations may be given, however. The stomata of the leaves are anomocytic and are not particularly sunken below the epidermis surface. There are two hair types: (1) ordinary filiform hairs consisting of 1, 2, or 3 cells, the terminal cell being the longest, and (2) small, stalked glandular hairs with a head consisting of a few cells standing parallel to the longitudinal axis of the hair. According to Herbst's

(1972) profound study, most of the vessels in the stem were observed to have scalariform perforation plates.

EMBRYOLOGY

The embryology seems to be entirely unknown and deserves being studied, especially with respect to endosperm formation and endosperm haustoria. (It is expected that the ovules are unitegmic and tenuinucellate, and that the endosperm formation is cellular; most likely terminal endosperm haustoria may be present.) The seeds are reported to contain endosperm.

POLLEN

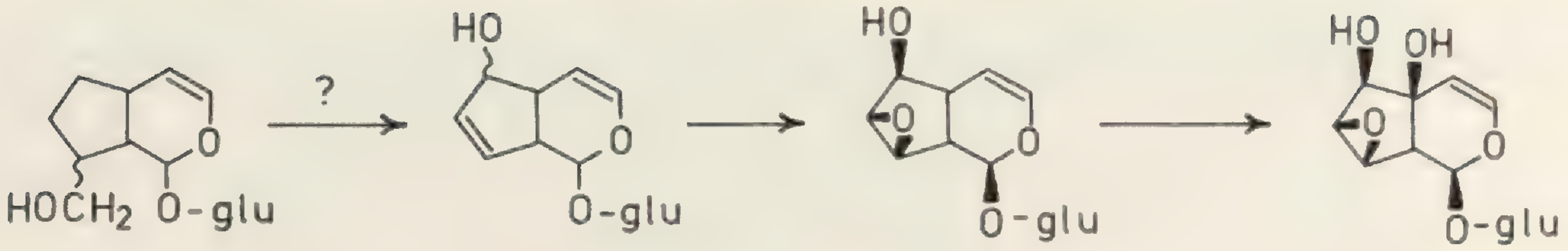
Pollen of *Retzia* is tricolporate with an obscurely delimited aperture and a microreticulate exine as reported by Punt & Leenhouts (1967) and by Goldblatt & Keating (1976). As reported by Goldblatt and Keating, the grains are spheroid equatorially, circular-semiangular in polar view and in size P = 35 μm, E = 30 μm. This type of pollen corresponds reasonably with Buddlejaceae, but not with most Loganiaceae. The large families Scrophulariaceae and Verbenaceae have a wide variety of pollen types, and grains similar to those of *Retzia* occur in several genera not otherwise related to *Retzia*. Pollen of Stilbaceae has not been much studied, but Erdtman's (1952) illustration of pollen of *Stilbe ericoides* is worth comparing with *Retzia*. Erdtman describes this as tricolporate, and prolate spheroidal, and in size, 18.5 × 17 μm. Pollen of *Retzia* and *Stilbe ericoides* can thus be said to be generally similar in morphology, though differing greatly in size.

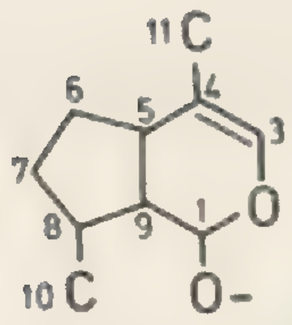
CYTOLOGY

Cytology is of little value in assessing the affinities of *Retzia*, which has $n = 14$, since almost all of the groups with which it has been allied are cytologically heterogeneous. In Lamiiflorae, with which *Retzia* exhibits strong chemical as well as morphological similarities, both Scrophulariales and Lamiales are cytologically diverse. In Scrophulariaceae, for which Raven (1975) tentatively postulated a base number of $x = 7$, there are numerous taxa that are fundamentally tetraploid with a frequent number of $n = 14$ and 12. Verbenaceae have an even wider range of chromosome number than Scrophulariaceae, both at diploid and tetraploid levels, with $n = 5, 6, 7, 9, 11–18$ well represented in various genera. Stilbaceae, believed to be very closely related to Verbenaceae, are cytologically unknown. Buddlejaceae, with which *Retzia* is often associated, is, in contrast, cytologically uniform with $x = 19$ in all genera so far examined, making this an unlikely ally.

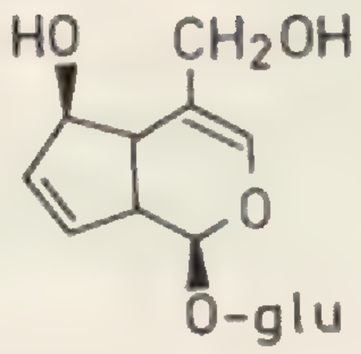
CHEMISTRY (IRIDOID GLUCOSIDES)

The presence of iridoids in *Retzia capensis* was demonstrated by Jensen et al. (1975), but, owing to scarcity of material, it was not possible at that time to identify any of the components.

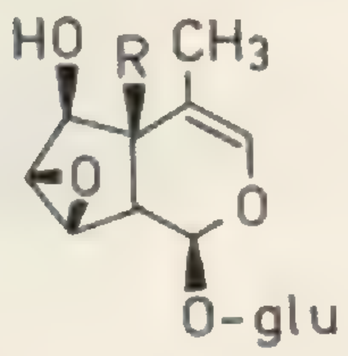




iridoid skeleton



5



6; R = H

7; R = OH

FIGURE 2. Upper row: Structures of the four iridoids occurring in *Retzia capensis*.—Lower row: Some biogenetically related iridoids, which as 2–4 in the upper row have lost C-10, but which have C-11 intact. They occur in Cornales and Loasales, which are no doubt related —though more distantly—to the Lamiales-Scrophulariales complex.

More material of the species has since become available and has been examined. Four iridoid glucosides have been isolated. Two of these have been identified, viz., unedoside (Fig. 2: 3) (mp, optical rotation and PMR-spectra of glucoside and its pentaacetate) and stilbericoside (Fig. 2: 4) (PMR-spectra and optical rotation of glucoside and pentaacetate, mp of pentaacetate). Tentative structures (Fig. 2: 1–2: 2) for the other two compounds are proposed on the basis of PMR-spectra and decoupling experiments. To our knowledge these two compounds have not been reported before as occurring in nature. Unedoside is known from *Arbutus unedo*, Ericaceae (Geissman et al., 1966) and from *Stilbe ericoides*, Stilbaceae (Rimpler, 1972), where it occurs together with stilbericoside (Rimpler & Pistor, 1974).

The compounds shown in Figs. 2: 2–2: 4 can be arranged in a very probable biosynthetic sequence, after which epoxidation of the 7, 8-double bond in compound 2 leads to 3, which is transformed into 4 by allylic oxidation at C-5. Whether 1 fits into this scheme is not easy to say, as nothing is known about the way in which C-10 is lost.

The compounds shown in Figs. 2: 5–2: 7 form a group of biogenetically related compounds, which like the *Retzia* compounds 2–4 have lost C-10, but in which C-11 is intact. It includes decaloside (5) in *Mentzelia* (Loasaceae), deutzioside (6) in *Mentzelia* and *Deutzia* (Hydrangeaceae), and scabroside (7) in *Deutzia*.

Details about the structure of the iridoids of *Retzia* will be published later.

A preliminary investigation of material of *Xeroplana gymnopharyngia* (Stilbaceae) indicates that this species also has quantities of stilbericoside as judging from the PMR-spectra.

POLLINATION

Retzia capensis is, at least to a great extent, bird pollinated. It has been

FIGURE 3. Approximate distribution of *Retzia capensis*. Based on information in Herbst's (1972) unpublished study on the species.

observed on several occasions to be visited by the orange breasted sunbird (*Anthobaphes violacea*) at Betty's Bay, Caledon District. The long tubular flowers also suggest bird or possibly advanced insect pollination. The flowers are protogynous. A noticeable detail is that the style, in the material studied by the authors, elongates more rapidly than the corolla tube. Therefore, in early flowering stage, the style reaches up to more than 10 mm out of the flower, while the corolla lobes are still mostly closed. Thus when sucking nectar a visiting bird or insect has great chances to touch the very minute stigmatic lobes. In a later flowering stage the introrse anthers stand well out of the floral tube between the lobes.

DISTRIBUTION AND ECOLOGY

Retzia capensis (according to Herbst, 1972) is restricted in its distribution to the Somerset West, Caledon and Bredasdorp districts, occurring from the Hottentots Holland Mountains (Sir Lowry's Pass–Elgin area) in the west and northwest, then along the Klein River, Houw Hoek Pass, and Babylons Tower Mountains, continuing eastwards along the Elandskloof Mountains to the Bredasdorp Mountain in the east (Fig. 3).

It grows on slopes of the Table Mountain sandstone, in sand or gravelly sand, often among rocks. It is fairly common locally in the Caledon and Bredasdorp districts. In certain areas it is threatened by repeated veld fires. Normally, veld fires at long intervals cause little harm, as *Retzia* withstands burning down to the root crown, from which branches can regenerate. It is also likely that seed

germination is rather favored by burning. Too frequent burning hinders the plants from reaching sufficient maturity to produce flowers and seeds, however, and can cause local extinction (Marloth, 1932).

Possible Affinity

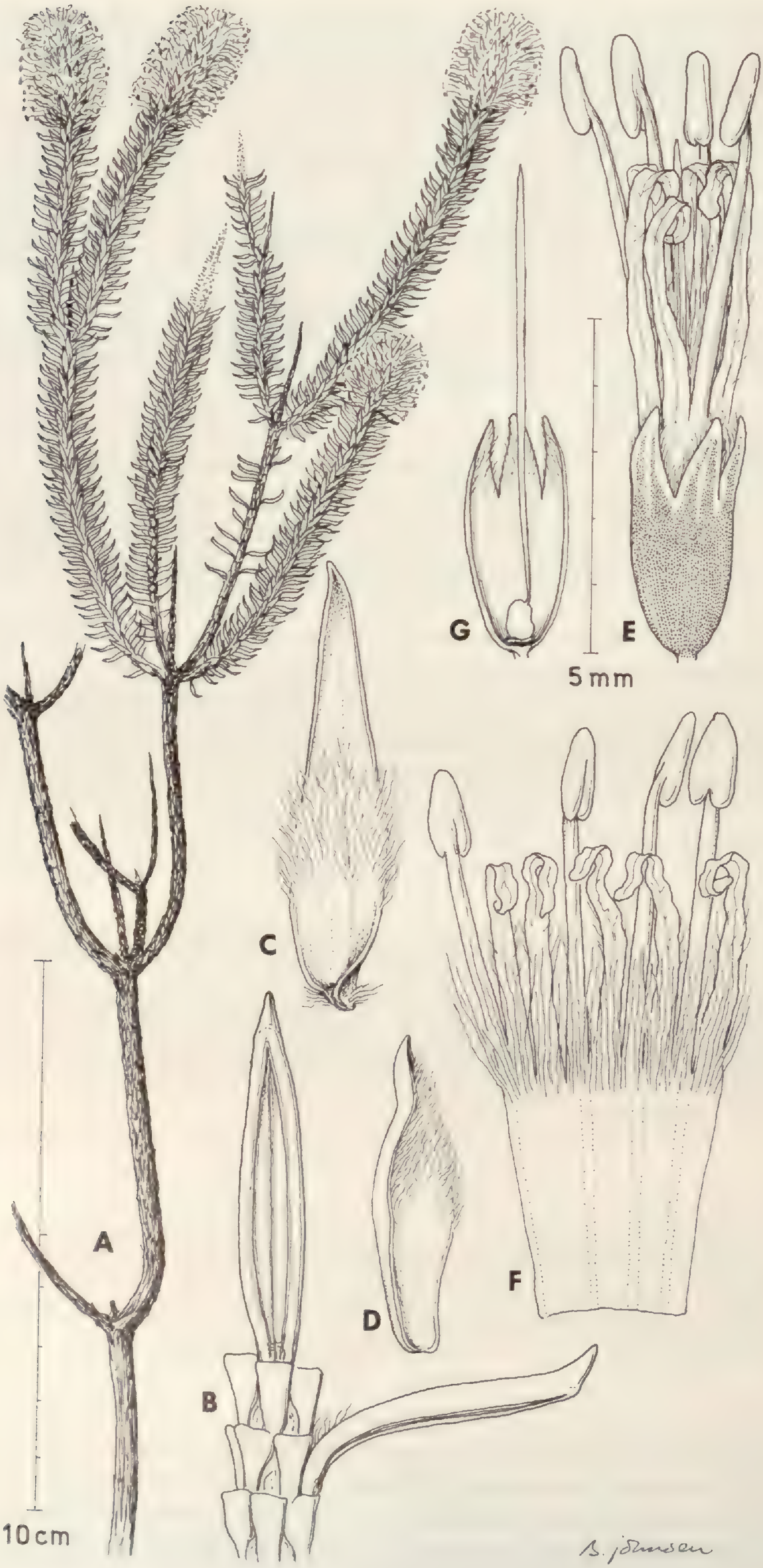
The evidence from the type of iridoids indicate that Retziaceae should be excluded from the Gentianales and adjacent orders (which may collectively be called Gentianiflorae), in which seco-iridoids are commonly present.

There is nothing, however, that militates against a position of Retziaceae in the Lamiiflorae, within which one may distinguish the closely related orders Lamiales and Scrophulariales. The close resemblance in iridoid contents (stilbericosid and unedoside are in common with *Stilbe*), focuses attention on groups like Stilbaceae, but also Scrophulariaceae, Selaginaceae and related families.

It may be of particular interest to compare *Retzia* with *Stilbe* (Fig. 4). This, with four more small genera, comprise Stilbaceae, a family at present being studied by Rourke. Like *Retzia*, the Stilbaceae is endemic to the Cape Region of South Africa.

The following features exhibit more or less pronounced similarities between *Retzia* and genera in Stilbaceae:

(1) The plants comprise woody shrublets.
(2) Intraxylary phloem is lacking.
(3) The leaves are verticillate.
(4) The leaves are also linear, sessile, entire and more or less sclerophyllous ("ericoid" in a wide sense); similar leaves occur in *Eustachys abbreviata* A. DC. (Stilbaceae).
(5) The inflorescence is spicate (although the spikes are suppressed and lateral in *Retzia*).
(6) The flowers are subtended by a large leaflike bract and also have 2 relatively large, leaflike bracteoles.
(7) The flowers are hypogynous.
(8) The perianth is 5-merous.
(9) The flowers may be nearly actinomorphic in both groups (although there is reduction of one stamen in Stilbaceae and a greater variation towards pronounced zygomorphy of the corolla and calyx in that group).
(10) The corolla is tubular and has a valvate (or reduplicate-valvate) aestivation.
(11) The stamens are inserted in the corolla mouth and have a similar anther construction.
(12) The pollen grains are similar, 3-colporate with punctate exine.
(13) There is a small annular disc surrounding the ovary base.
(14) The pistil is 2-carpellate, completely or incompletely bilocular, with a single filiform style and a small stigma.
(15) The fruit may be capsular (or often indehiscent in Stilbaceae).
(16) The seeds contain endosperm.


A
B
C
D
E
F
G
10 cm
5 mm

(17) The iridoid compounds present are similar.
(18) The distribution is similar.

This list may seem impressive, but several differences may also be noted, such as:

(1) The more reduced and lateral spikes of *Retzia*.
(2) The much smaller flowers with weaker petals in Stilbaceae.
(3) The 4 instead of 5 stamens in Stilbaceae.
(4) The greater tendency for floral zygomorphy, sometimes also reduction, in number of petal lobes, in Stilbaceae.
(5) The few to solitary ovules in Stilbaceae, where one locule of the ovary may be empty. In this family the typical, pendulous ovules found beside the ascending ones in *Retzia* are lacking.
(6) The punctate stigma in Stilbaceae.

These differences in the authors' opinions seem rather insignificant relative to the similarities enumerated above. The affinity between Stilbaceae and Verbenaceae also needs to be further investigated. Stilbaceae certainly appears to be distinct from other Verbenaceae and thus merits family rank.

Poetically enough, *Retzia* was described by Marloth (1932) as "a living witness of the relic nature" of the Cape flora. There is no doubt that it is primitive in some characters, such as the scalariform perforation of the vessels and the ovules which are of both the ascending and the pendulous kind. This type by reduction of either the ascending or the pendulous kind could result in the ascending ones only (as in Stilbaceae) or the erect only (as in Selaginaceae). Another primitive state is the isomerous unreduced androecium and the nearly actinomorphic calyx and corolla.

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Figure 4. *Stilbe vestita* Berg.—*Dahlstrand 1015* from the Cape of Good Hope Nature Reserve, Cape Peninsula, South Africa, 1966.—A. Branch in the flowering stage.—B. Section of branch showing a leaf and also the subverticillate leaf insertion and the prominent stem ridges.—C. Bract, adaxial side.—D. Bracteole, adaxial side.—E. Flower, bracteoles removed.—F. Corolla opened, seen from the inside; notice that there are only 4 stamens.—G. Calyx in longitudinal section and the somewhat unsymmetrical pistil.—Del. Bent Johnsen.

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ANATOMICAL SUPPORT FOR THE TAXONOMY OF *CALOPHYLLUM* (GUTTIFERAE) IN PANAMA[1]

W. G. D'Arcy[2] and Richard C. Keating[3]

Abstract

Leaves of eight species of *Calophyllum* growing in Panama were sectioned and characterized anatomically. A number of characters seemed useful in clarifying the taxonomy and evolution of the genus. Apparently useful characters at the species level include midrib shape, primary vein "V" angle, presence or absence of transcurrent ducts, and presence or absence of a hypodermis. The species *C. nubicola* D'Arcy & Keating is described. Taxonomic relationships among the Panamanian species have been clarified. Old World species introduced into Panama can be distinguished anatomically, but they are not separable statistically as a group from New World species examined.

The genus *Calophyllum* comprises well over 100 species of New and Old World flowering plants. In preparing the treatment of the genus for the *Flora of Panama*, species were difficult to separate on herbarium morphological evidence, so anatomical studies of leaves were undertaken. Such studies had been used to good advantage in the Guttiferae by Vesque (1889, 1893), Schofield (1968), and Stevens (1974, 1976). Smith & Darwin (1974) discussed anatomy of the fruit, but only Vesque had touched on plants of the New World. Although Vesque established three sections for Old World species of *Calophyllum*, he did not classify the New World species into sections. Our anatomical studies summarized in Table 1 tended to confirm tenuous conclusions drawn from study of herbarium sheets, and they suggested changes that might not otherwise have been made, namely, recognition of a new species and separation of *Calophyllum rekoi* and Panamanian plants formerly known as *C. longifolium* from *C. brasiliense*. They also showed the anatomical basis for the leaf ribs which are a useful taxonomic character. A less satisfactory conclusion is that two specimens studied in detail cannot be assigned to any of the known species from Panama, and the herbarium material is insufficient for description of new species. While it is possible that these species have already been described based on material from other countries, our investigations suggested no likely candidates among the relatively few species that have been described from the New World. These results suggest that further realignments will be required, but these possibilities could not be pursued within the limitations of this study.

Materials and Methods

Following careful study of material available from several herbaria (A, F, GH, MO, DUKE, PMA, SCZ, US) a number of elements were selected for

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anatomical study. This selection included specimens of plants believed to be native to the neotropics, and two species known to have been introduced into cultivation from the Old World. One of these Old World species, *C. inophyllum*, has been studied anatomically by several other workers so this species provides a reference of our work to that of others.

Specimens of leaves of eight species of *Calophyllum* were removed from nine herbarium collections (see Table 1) and restored using Aerosol OT (Ayensu, 1967) at 45°C for one week. Two pieces from approximately the center of each leaf were selected and oriented to produce transverse sections of the midrib and transverse sections of the parallel secondary veins. Following restoration, the specimens were fixed in 50% formalin-propiono-alcohol, dehydrated in a tertiary butyl alcohol series (Johansen, 1940), embedded in Paraplast and sectioned at 10 μm. The sections were stained in Safranin O-Fast Green FCF and photographed at 100× magnification. Drawings of the midrib areas were made using a microprojector.

Hand sections were made of leaves of many other available specimens to confirm results drawn from paraffin sections. In addition counts of vein frequency were made of all specimens available.

Gross Morphology

Calophyllum embraces species of trees and shrubs, some of them large and dominant in tropical forests. They sometimes have buttressed bases and the sap is usually milky or yellow. The leaves are entire, usually coriaceous and petiolate. Most treatments in the past have relied heavily on leaf characters, often involving internal anatomical details which are not readily observable. Some species are sparingly pubescent but little taxonomic use has been made of hairs, nor does the inflorescence appear to be a useful character. Interpretation of the perianth is subject to argument, but flowers of most Old World species are usually considered to have petals, while New World species all lack petals. Otherwise there is remarkable similarity in the flowers. The fruits offer a number of taxonomic characters: size, shape, surface appearance, and the size of the seed relative to the locule are all useful, but as fruits are lacking on most herbarium specimens, other characters must be sought for routine determination of specimens.

Anatomical Characters

Histological features of leaves of *Calophyllum* and most other Guttiferae are more regular and highly organized than those found in the majority of mesic dicotyledons. As Stevens (1974) found, midrib type and venation prominence are associated with histological features, and most species can be recognized from leaf sections. The following features appear to be of systematic importance in *Calophyllum* leaves.

Leaf transverse sections, general histology

The leaves are bifacial. The midrib shape is systematically variable and the transectional aspect of the included tissues varies with the midrib shape. The

TABLE 1. Anatomical characteristics of *Calophyllum* leaves

Taxa	Specimen	Midrib Sclerenchyma an Inverted "Y"	Hypodermis	Vein frequency/height ratio	Duct Position[a]	Ducts Transcurrent	Duct Diameter (μm)	Sclereids below Ducts[b]	Ribs per cm	Thickness							
										Lamina	Adaxial Epidermis	Cuticle	Abaxial Epidermis	Mesophyll	Palisade	Spongy	Hypodermis
NEW WORLD																	
1. *C. angulare*	*Krukoff 1442*	+	−	0.75–1.0	M	−	20–30	(2)	44	310	20	2	20	250	90	160	−
2. *C. brasiliense*	*Claussen 237*	−	+	1.7	M	−	80–90	−	15–18	320	20	2	15	230	80	150	15
3. *C. longifolium*	*Croat 8532*	+	+	2.0	M	+	50–70	(3)	22–27	320	25	5	15	260	80	180	10
	Lao 571	+	+	2.0	M	+	50–70	(3)	28	280	15	1	10	210	90	120	10
	Foster 1480	+	+	1.0–1.5	M	+	50–70	(3)	25	425	30	2	20	370	80	260	20
	Croat 6451	+	+	1.5	M	+	50–90	(3)	25	470	40	15	15	350	70	280	25
	Pittier 6597	+	+	1.0	M	+	50–70	(3)	35	500	20	10	15	400	150	250	20
	Stimson 5132	+	+	1.0	M	+	60–70	(3)	30	500	20	10	12	420	150	220	25
4. *C. nubicola*	*Dwyer et al. 7301*	+	−	0.7–0.9	H	−	40	+	34–36	400	20	5	20	340	110	230	−
	Mori & Kallunki 6508	+	−	0.8–1.0	H	−	60–80	+	30	390	25	4	15	350	70	270	−
5. *C. rekoi*	*Calderón 147*	−	−	2.0–2.5	M	−	40–50	−	24–27	230	25	1	15	160	60	110	−
	Reko 3557	−	−	2.0–2.5	M	−	40–50	−	17–20	225	20	2	15	180	70	150	−
	Dwyer 1670	+	−	1.5–2.0	M	−	50–60	−	20–25	290	12	5	12	200	70	150	−
	Holdridge 6232	−	−	2.5–3.0	M	−	40–50	−	30	200	15	1	20	140	40	80	−
6. *C. calaba*	*Wagner 1611*	−	−	3.0–4.0	M	−	60–90	−	12–15	300	25	4	20	216	55	160	−
	Liesner 4881	−	−	3.0–4.0	M	−	50–60	−	20	230	25	4	15	180	70	120	−
OLD WORLD																	
7. *C. soulattri*	*Pittier 6678*	+	+	2.5–3.0	M	+	40	(3)	39–40	270	10	1	10	190	60	130	10
8. *C. inophyllum*	*Nee 11420*	−	−	1.7–2.0	M	−	70	−	10–14	350	20	2	15	280	70	210	−
	Standley 30868	−	−	2.0–2.5	M	−	80–90	−	18–20	270	20	2	20	212	40	160	−

[a] M = medial, H = high.
[b] (2) = nests of fibers where sclereids may occur in other species; (3) = fibers around transcurrent ducts.

midrib is prominent abaxially, either rounded or 1–3-angled. An adaxial ridge or depression may also be present. No palisade layer or other mesophyll is present above or below the midrib. Vascular bundles are collateral. Xylem of the midrib forms a sharp V-shape or transitions to a wide rounded arc or crescent. The angle of the "V" varies from 45° to 90°. On the adaxial side, two patches of fibrous sclerenchyma are attached to the ends of the xylem and adaxial to it (Figs. 2, 7–9), or the fibers may form a continuous inverted "V" running into the adaxial midrib ridge (Figs. 1, 3–5). Secretory ducts may be present above or below the vascular bundle within the ground tissue.

Cross-sections of the lamina cut perpendicular to the secondary veins are bounded by well-cuticularized epidermal layers on both surfaces. Outer walls are well cuticularized with cuticular ridges (flanges) often running between epidermal cells. Stomata are common and level with the abaxial epidermis. An adaxial hypodermis of one layer is present in some species.

Secondary veins are regularly spaced and parallel to each other from the base to the apex of the leaf. They leave the midrib at a uniform acute angle and are always transcurrent with ridges of fibers, 1–3-seriate, running to both epidermal layers. Spacing of secondary veins appears to be species specific (Smith & Darwin, 1974; Stevens, 1974, 1976) and has been expressed here as veins per cm and as the frequency/height ratio. The veins vary from closely spaced (the distance between them being less than the measure of their height, 0.7–1.0:1) or widely spaced, the distance between veins being 1–4 times their height (1–4:1).

The palisade may be 1–3 layers deep over a loosely arranged spongy layer which occupies more than half of the total mesophyll. Secretory ducts are present in all specimens, equidistant between and parallel to the secondary veins. On surface view, transcurrent veins and ducts often look alike and may be indistinguishable. They appear as ribs whose frequency can be counted. This measure, expressed as ribs per cm, may include veins alone or equal proportions of veins and ducts. Without transcurrent sclerenchyma, the ducts are referred to as embedded (Stevens, 1974). The duct lumen may be medially placed between the epidermal surfaces or it may be high (closer to the adaxial epidermis). Duct size and placement appear to be systematically valuable characters.

Sclereids may be present in the spongy layer abaxial to the embedded ducts. Druse crystals and occasionally prisms range from absent to common in ground tissue of the midrib or in the lamina. When present, they are usually within the palisade layer.

Previous writers have commented on the constancy of anatomical characters. Thus Vesque (1893: 533) insisted that the presence or absence of hypoderm is constant for a given species, but he believed that other characters must be considered more of a quantitative than a qualitative nature. Nevertheless, he did not hesitate to rely on other anatomical characters to distinguish species in his key and descriptions. Stevens (1974: 350) stated: "Nearly all species of *Calophyllum* can be recognized by their leaves alone in both the field and the herbarium. Apart from shape, toughness, size, the prominence of the margin and to a certain extent the colour of the leaf on drying, the characters which give the leaf its characteristic look are the midrib and venation." Then he noted that

while these characters are usually fairly constant, they are subject to variation, sometimes even on a single specimen. "Anatomical differences on the whole correlate well with morphological differences and most species can be recognized from sections of the leaves" (p. 352). He was able to prepare a key to *Calophyllum* in Papuasia without relying on anatomical characters, but he did include measurement of vein frequency in his species descriptions, and he sometimes presented other details including, for example, thickness of epidermal cells, angle of midrib bundle divergence, number of veins or latex canals enclosed by the marginal thickenings, etc. Our study does not include a large enough sample to warrant firm statements as to the qualitative nature or specific constancy of any characters, and in the absence of such statements by previous workers such as that of Vesque regarding hypoderm, we must regard all statements regarding individual characters as generalizations to be subjectively judged. Many of the characters we have observed appear to be species specific, but a wider range of material must be examined before their variation can be assessed.

1. *Calophyllum angulare* A. C. Smith, Bull. Torrey Bot. Club 60: 379. 1933. TYPE: Brasil, Matto Grosso, *Krukoff 1442* (MO). FIG. 1.

MIDRIB prominent abaxially, 3-angled with a V-shaped median ridge, raised adaxially in a truncated ridge. *Xylem* forms a prominent V shape. Bundle angle 45–50°. *Sclerenchyma* of fibers forming an inverted V extending into the adaxial ridge. *Secretory ducts* small in the ground tissue.

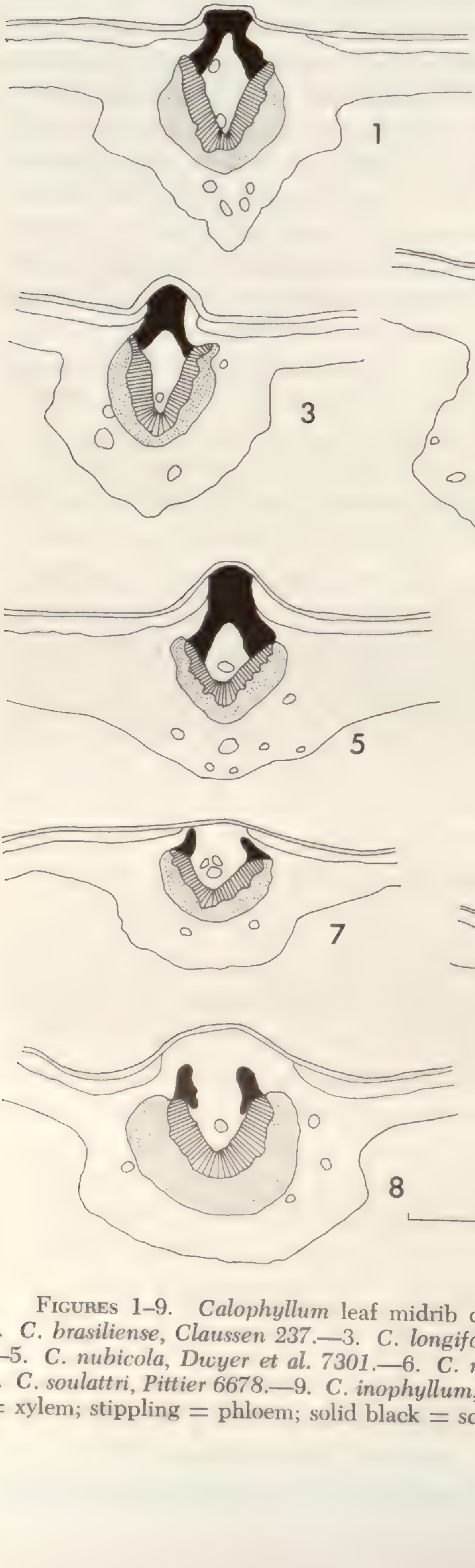
LAMINA. *Adaxial* and *abaxial epidermal layers* of equal thickness. *Veins* transcurrent and closely spaced. Frequency/height ratio 0.75–1:1. *Hypodermis* absent. *Palisade* in 2 layers occupying 40% of the mesophyll. *Secretory ducts* small and equidistant between the epidermal surfaces. Four–six large-lumened fibers abaxially adjacent to each duct. *Crystals* not seen. *Sclereids* absent.

The type collection of *C. angulare* was selected because it superficially resembles some of the non-Barro Colorado Island specimens now known to be variants of *C. longifolium*. The specimen differs from Panamanian *C. longifolium* anatomically in lacking a hypodermis, in having closer veins in relation to lamina thickness, in lacking transcurrent ducts and hence in having fewer ribs per centimeter, in having narrow ducts, and in lacking sclereids. The disjunction which would result from considering this Brazilian species conspecific with Panamanian *C. longifolium* is also quite improbable.

Specimen examined: *Krukoff 1442* (MO).

2. *Calophyllum brasiliense* Camb. in St. Hil. et al., Fl. Brasil Mérid. 1: (ed. folio, MO copy) 247, *tab. 67*. 1827. TYPE: Brazil, Espiritu Santo, *St.-Hilaire 330* (P, not seen, photo MO). FIGS. 2, 14.

MIDRIB rounded abaxially and flat or slightly concave adaxially. The midrib of this specimen agrees with *C. brasiliense* as figured by Schofield (1968). *Xylem* forms a low crescent-shaped arc. Bundle angle 85–90°. *Sclerenchyma* of fibers



FIGURES 1–9. *Calophyllum* leaf midrib cross-sections.—1. *C. angulare, Krukoff 1442.*—2. *C. brasiliense, Claussen 237.*—3. *C. longifolium, Lao 571.*—4. *C. longifolium, Croat 8532.*—5. *C. nubicola, Dwyer et al. 7301.*—6. *C. rekoi, Reko 3557.*—7. *C. rekoi, Calderón 147.*—8. *C. soulattri, Pittier 6678.*—9. *C. inophyllum, Nee 11420.* Scale line equals 1.0 mm. Hatching = xylem; stippling = phloem; solid black = sclerenchyma.

forming 2 patches adaxial to the ends of the xylem. *Secretory ducts* present in the ground tissue.

LAMINA. *Adaxial epidermis* thicker than the abaxial epidermis. *Veins* transcurrent, widely spaced. Frequency/height ratio 1.7:1. *Hypodermis* present. *Palisade* parenchyma in 2 rows occupying 40% of the mesophyll. *Secretory ducts* very large, equidistant between the epidermal surfaces. No sclerenchyma near the ducts. *Druses* present but uncommon. *Sclereids* absent.

The specimen examined was the only one available which had been annotated by Vesque as *Calophyllum brasiliense* subsp. *verum* var. *α genuina*. It was examined to confirm whether *C. longifolium* and *C. rekoi* could reasonably be considered conspecific with *C. brasiliense* as was affirmed by Vesque (1893) and by Standley (1932) and followed by subsequent workers. The specimen was collected in Minas Gerais but no other collection data are available. This same specimen was examined and figured by Vesque (1889, 1893).

The material examined of this species differs from *C. rekoi* in having a hypodermis and in having very large ducts in the lamina. It differs from Panamanian *C. longifolium* in details discussed under that species.

Specimen examined: Brazil, Minas Gerais, *Claussen 237* (MO).

3. *Calophyllum calaba* [Plum.] L., Sp. Pl. 514. 1753. LECTOTYPE: *Calaba* Plum., Pl. Nouv. Amér. Gen. 39, *tab. 18*. 1703.

MIDRIB prominent abaxially, rounded to slightly 3-angled, adaxially with a slight groove. *Xylem* forms a V shape. Bundle angle of 70–80°. *Sclerenchyma* of fibers forming 2 small patches of thick-walled cells attached at the ends of the xylem strands; in addition, much of the tissue of larger-lumened cells beneath the adaxial surface of the midrib are lignified. *Secretory ducts* are few and large in the ground tissue.

LAMINA. *Adaxial* and *abaxial epidermal layers* of equal thickness. *Veins* transcurrent and widely spaced. Frequency/height ratio 3–5:1. *Hypodermis* absent. *Palisade* of 1 layer occupying 25–40% of the mesophyll. *Secretory ducts* large and equidistant between epidermal surfaces; ducts may be partially encircled by a single sheath of fibers with the sheath having no consistent orientation. *Druses* common in the palisade layer. *Sclereids* not seen.

Typification of this name has been subject to controversy and confusion in the past, but most writers, both ancient and recent, have applied the name to plants of the Caribbean based on either Plumier or Jacquin descriptions. Furtado (1941) and Howard (1962) have discussed the merits of this choice of name, and it is in this Antillean context that we use the name here. The species is recognizable by its widely spaced ribs, small rounded leaves, and short petioles, and anatomically by its widely spaced ribs and lack of hypodermis. No specimens of this species have been seen from Panama. *Liesner 4881* from neighboring Costa Rica appears to be a good representative of *C. calaba*. It is from Guanacaste Province which is subject to seasonal drought, a condition also prevailing in much of the Antillean region. Anatomically it compares well with *Wagner 1611* from Puerto Rico.

Specimen examined: Costa Rica, *Liesner 4881* (MO). Puerto Rico, *Wagner 1611* (MO).

4. *Calophyllum inophyllum* L., Sp. Pl. 513. 1753. TYPE: East Indies, Herb Linn (LINN 676.1, not seen; microfiche MO). FIGS. 9, 12–13.

MIDRIB prominent, strongly V-shaped abaxially, no protrusion or concavity adaxially. *Xylem* forms a V-shaped strand. Bundle angle 60–62°; Stevens (1974) records a bundle angle of 70–90°. *Sclerenchyma* of fibers forming 2 small patches attached to the ends of and adaxial to the xylem. *Secretory ducts* small, frequent in the ground tissue of the midrib.

LAMINA. *Adaxial* and *abaxial epidermal* layers of equal thickness. *Veins* transcurrent, widely spaced. Frequency/height ratio 1.7–2:1. *Hypodermis* absent. *Palisade* in 2 layers occupying 30% of the mesophyll. *Secretory ducts* large, between the secondary veins and equidistant between the epidermal surfaces. No sclerenchyma associated with the ducts. *Druses* and *prismatic crystals* common in the ground tissue of the midrib. *Sclereids* absent.

This species is widespread on coastal sites in the Indian Ocean and South Pacific, and it has been introduced into the New World as a cultivated street tree. It resembles some collections of *C. longifolium* but is easily distinguished by having petals and fewer leaf ribs than any other Panamanian element. This species was studied by Kienholz (1926), Stevens (1974, 1976), and Vesque (1889, 1893), and our inclusion of it was in part to relate this study to previous work. Our observations agree with those of previous descriptions. *Calophyllum inophyllum* has a strikingly different midvein shape from other species studied. Anatomically, the combination of having no hypodermis, no inverted V sclerenchyma, no transcurrent ducts, and no sclereids is unique to this species.

Specimens examined: Panama, Canal Zone, cultivated, Ancón, *Nee 11420* (MO).

5. *Calophyllum longifolium* Willd., Ges. Naturf. Freunde Berlin Mag. Neusten Entdeck. Gesammten Naturk. 5: 80. 1811. TYPE: America meridionalis, Herb. Willd. 10117 (B-Willd., not seen; microfiche MO). *C. brasiliense* subsp. *longifolium* (Willd.) Vesque, in D.C., Monogr. Phan. 8: 592. 1893. FIGS. 3–4, 11.

MIDRIB prominent abaxially, 3-angled with a V-shaped median ridge, raised adaxially in a smaller truncated or rounded ridge. *Xylem* forms a V-shaped strand. Bundle angle 45–55°. *Sclerenchyma* of fibers forming an inverted V extending into the adaxial ridge. *Secretory ducts* few or numerous in the midrib ground tissue.

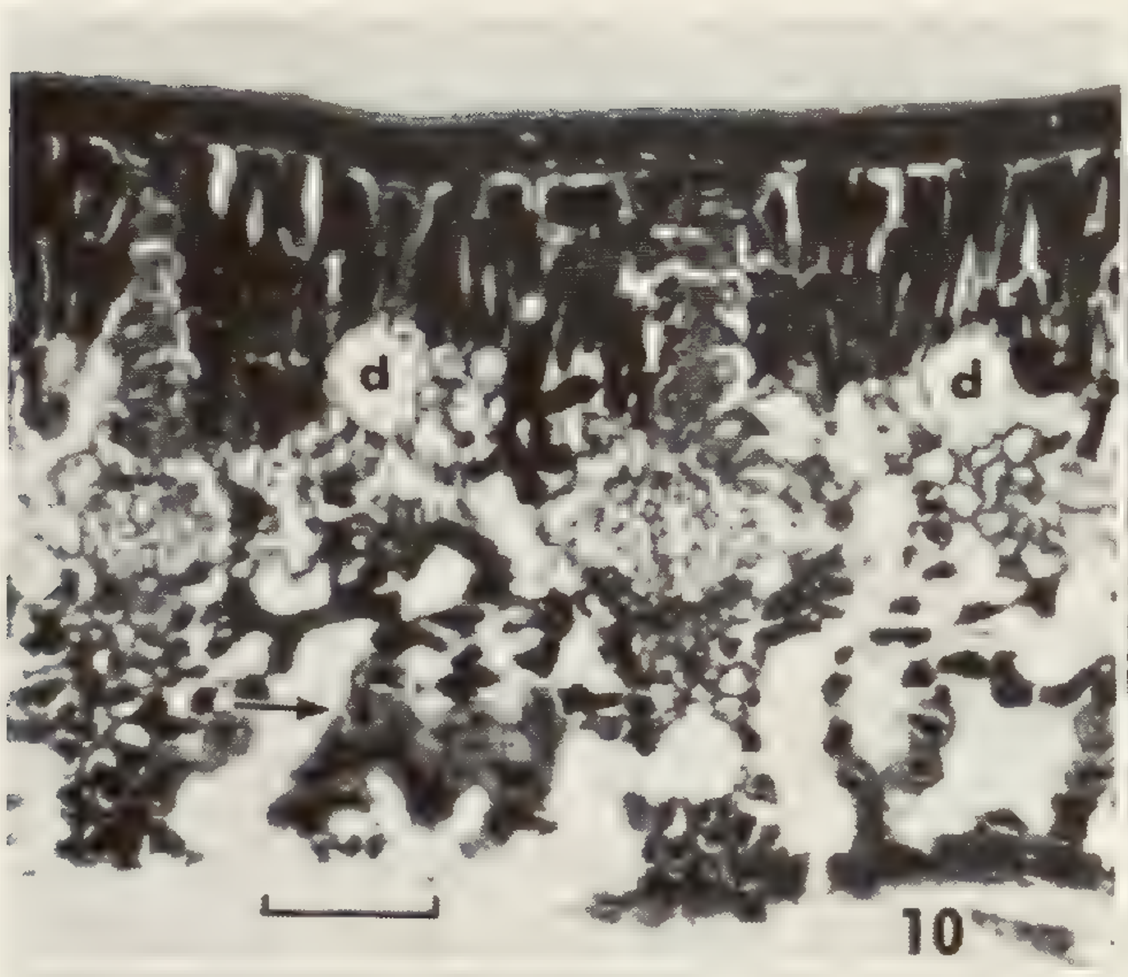
LAMINA. *Adaxial epidermis* about twice as thick as the abaxial. *Veins* transcurrent, widely spaced. Frequency/height ratio 2:1. *Hypodermis* present. *Palisade* in 1–2 layers occupying 30–50% of the mesophyll. *Secretory ducts* large, between the secondary veins and weakly or strongly transcurrent. *Druses* uncommon or common in the mesophyll or in the midrib ground tissue. *Sclereids* absent or present as 1–2 cells in the spongy layer near the abaxial epidermis.

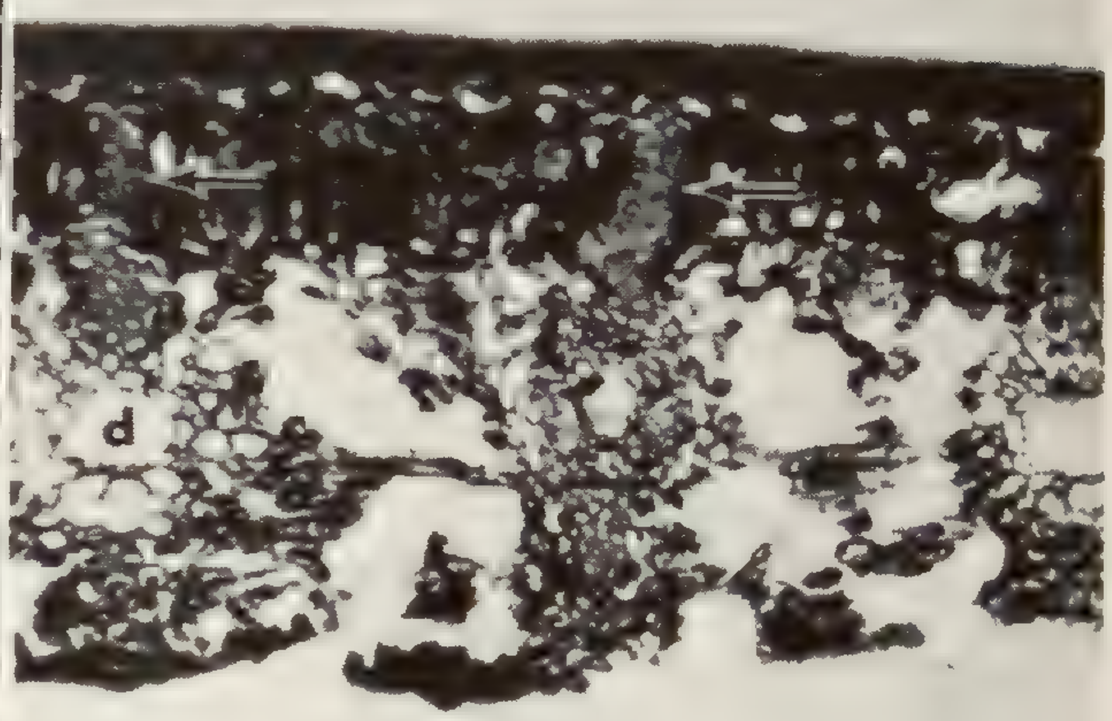
Calophyllum longifolium can be distinguished by the number of leaf ribs

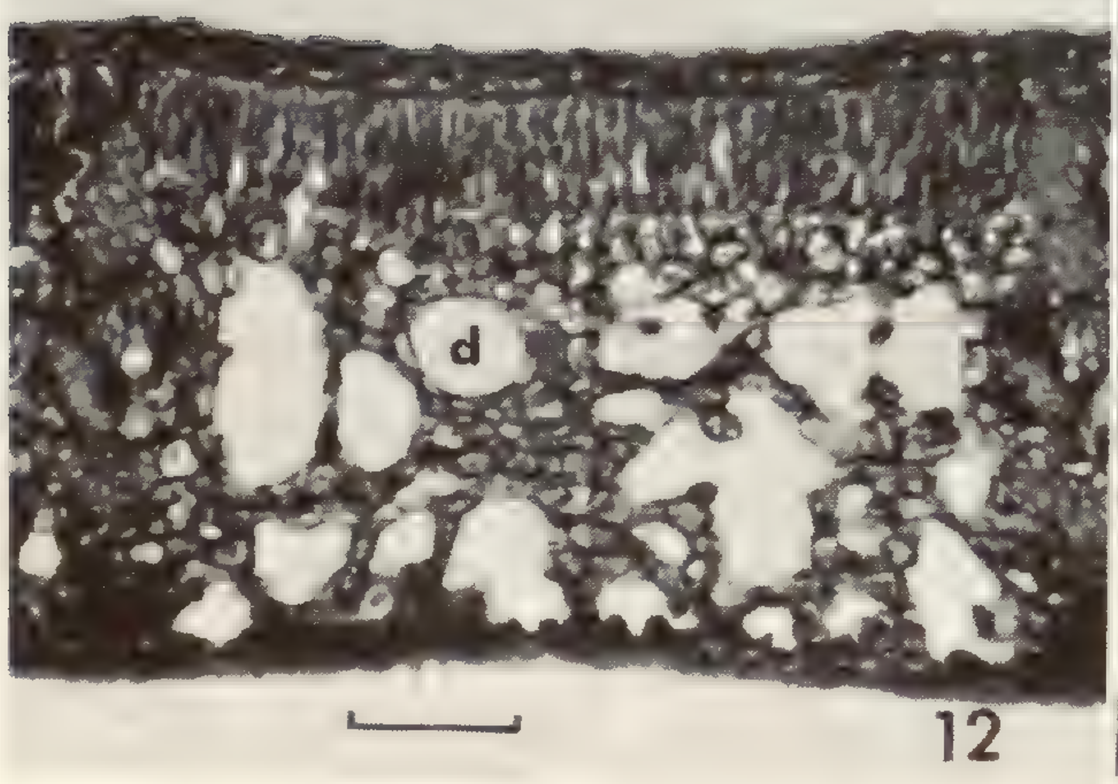
and by the structure of the fruit (to be discussed in the *Flora of Panama*). The numerous collections from Barro Colorado Island suggest a uniform species native to lowland Panamanian forests. However, collections taken from other parts of the country are not all superficially similar, and some have been annotated by Bassett Maguire, longtime specialist in the group, as *C. brasiliense* var. *rekoi* (Standl.) Standl.

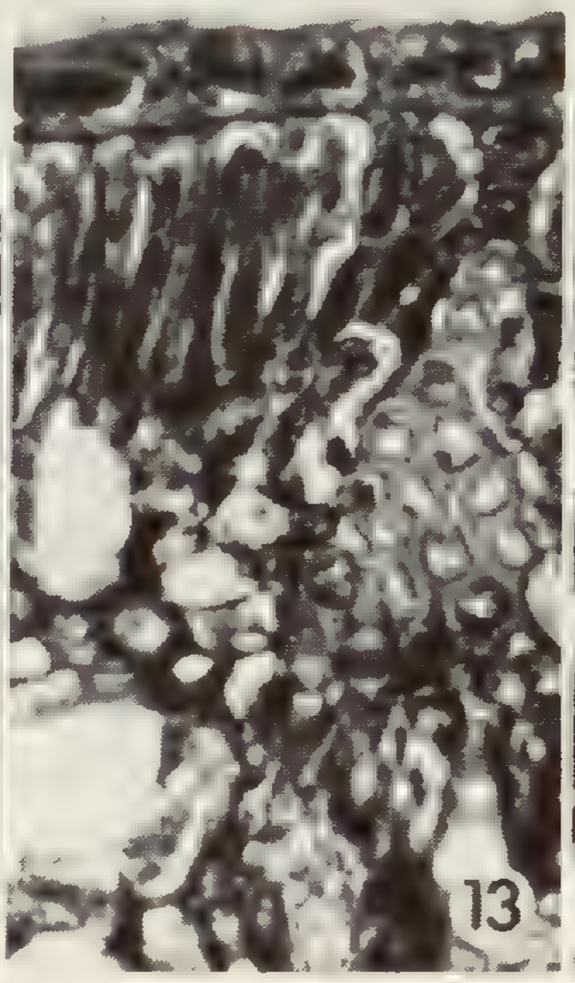
The name *Calophyllum longifolium* is applied to Panamanian plants with considerable reservation. The name was published with scant description and the source is broadly indicated on the original collection as *America meridionalis*. Later, Kunth (1821) used the name for a sterile Humboldt & Bonpland specimen from Peru, but, although he expressed doubt that the plant was a *Calophyllum*, the photo (MO) closely resembles the plants from Panama we are calling *C. longifolium*. Planchon & Triana (1861: 253) noted that Choisy had annotated a specimen, probably a duplicate of *Claussen 237* (see above under *C. brasiliense*), as *C. calaba* var. *longifolia*, but they disagreed with this disposition arguing that the specimen is really *C. brasiliense*. Planchon & Triana (1861: 255) then assigned two other specimens to *C. longifolium*, one the specimen treated by Kunth, and the other a specimen at MPU from Panama. Somewhat later Vesque (1893: 592) reexamined both specimens cited by Planchon and Triana and on this basis placed *C. longifolium* at subspecific rank under *C. brasiliense*, adding a specimen from Jamaica to his list of material seen. None of these writers except Kunth had opportunity to examine the original specimen which is still preserved in Willdenow's herbarium at Berlin, and hence their detailed analysis cannot be used to justify use of the name *C. longifolium*. We have seen the microfiche of the Willdenow specimen and have had the use of a pencil rubbing kindly put at our disposal by Peter Stevens. This specimen has leaves much like the abundant collections from Barro Colorado Island, Panama, but there are only 17–20 ribs per cm, fewer than is usual in the Panamanian plants, and in the same range as *C. rekoi*. The petioles are shorter, and Stevens noted that the twig is glabrous, while in the Panamanian plants the twigs and petiole undersides are minutely puberulent. However, being unable to examine the type collection personally, we are unwilling to affirm that it is not the same as the Panamanian plants. Such an affirmation would require a new name for the Panamanian element, and we would have to find another Central American species to which the name could confidently apply.

Calophyllum longifolium differs from both *C. brasiliense* and *C. rekoi* in several respects, which we believe to be significant at the species level. From *C. brasiliense* it differs in having transcurrent ducts, in having more frequent veins, in the midrib sclerenchyma forming an inverted V, and in having sclereids. It also has smaller ducts, slightly thicker lamina, cuticle, mesophyll, and thinner hypodermis. From *C. rekoi*, *C. longifolium* differs in having a hypodermis, in having the midvein sclerenchyma in a V, in having transcurrent ducts, in having sclereids, and it also has slightly larger ducts, and much thinner lamina, cuticle, mesophyll, spongy mesophyll, and slightly thinner palisade tissue. We can see no justification for considering these three elements as conspecific as Vesque and Standley have done in the past.









Figures 10–14. Cross-sections of *Calophyllum* leaves perpendicular to the secondary veins. —10. *C. nubicola, Dwyer et al. 7301.* Note small ducts (d) between transcurrent veins and above the center of the leaf. Note sclereids (arrow) below the ducts.—11. *C. longifolium, Croat 8532.* Both veins and ducts (d) are transcurrent (arrows).—12. *C. inophyllum, Nee 11420.* Duct (d) is not transcurrent and is centered between the epidermal layers.—13. *C. inophyllum, Nee 11420.* Note absence of a hypoderm over the palisade layer.—14. *C. brasiliense, Claussen 237.* Note hypoderm over the palisade layer. Scale lines equal 100 μm.

Specimens examined: Panama, Canal Zone, Barro Colorado Island, *Croat 8532* (MO); *Foster 1480* (SCZ); *Croat 6451* (MO, SCZ). Darién, *Pittier 6597* (US); *Stimson 5132* (GH). Herrera, El Monteroso–Las Minas, *Lao 571* (MO).

6. *Calophyllum nubicola* D'Arcy & Keating. TYPE: Panama, *Mori & Kallunki 7301* (MO). Figs. 5, 10.

Arbor ve arbuscula ad 12 m altus. Folia coriacea, parva, plana, rugis lateralis obscuris, 34–36 per cm. Fructus globusus, apiculatus, semine loculum ⅘ inplenti.

Tree or *shrub* to 12 m tall, much branched, the twigs slender, stiff, ascending, drying yellowish or reddish brown but soon greyish, scruffy. *Leaves* elliptical, sometimes broadly so, small, to 6 cm long, 4.5 cm wide, stiffly coriaceous, plane but the margins minutely revolute, the costa conspicuous, subplane or elevated above, rounded to sharply raised beneath, evanescent distally, drying reddish

brown, the lateral ribs somewhat obscure and appearing very numerous, actually 34–36 per cm, usually more distinct above; petiole 5–10 mm long, drying ca. 2 mm thick, with a narrow groove above. *Inflorescence* not seen. *Fruits* globose or slightly ellipsoidal, 20–25 mm long, conspicuously apiculate, the apicule 2–4 mm long, longer than broad, the basal stipe resembling the apicule, the surface drying glaucous, reddish brown, wrinkled; fruiting pedicels 10–12 mm long, resembling the twigs; interior wall of the fruit papery, thin, dark brown, the endocarp stony; seeds globose, brown, occupying ⅘ of the locule.

This species is known only from Cerro Jefe, a lowland cloud forest reaching ca. 900 m elevation just northeast of Panama City. Woody plants in this habitat have notably coriaceous, small, entire leaves and much-branched twigs.

Midrib rounded abaxially and raised adaxially into a narrow, rounded ridge. *Xylem* forms a broad V. Bundle angle 70–75°. *Sclerenchyma* of fibers forming an inverted V extending upward into the adaxial ridge. *Secretory ducts* common in the ground tissue of the midrib.

Lamina. *Adaxial epidermis* slightly thicker than the abaxial. *Veins* transcurrent, closely spaced. Frequency/height ratio 0.9:1. *Hypodermis* absent. *Palisade* cells in 2(–1) layers occupying 30% of the mesophyll. *Secretory ducts* small, between the transcurrent veins and closer to the adaxial epidermis at the boundary of the palisade and spongy layers, not transcurrent or associated with sclerenchyma. *Druses* and prismatic crystals common in the ground tissue of the midrib, uncommon in the mesophyll. *Brachy-* and *macrosclereids* forming prominent groups in the spongy mesophyll beneath the ducts.

This species is distinctive in its small flat leaves and in the much-branched appearance of the specimens. The lateral venation is obscure and the ribs are difficult to count. The seed is loose and rattles inside the fruit, but it fills over ⅘ of the locule. There is no spongy tissue in the unfilled portion of the locule. *Calophyllum nubicola* superficially resembles *C. angulare*, but differs in its smaller, more coriaceous, more rotund leaves with numerous, obscure ribs. The twigs are narrower and the petioles are shorter. Anatomically, the laminar secretory ducts of *C. nubicola* are situated closer to the adaxial epidermis than in any other species. Sclereids in *C. nubicola* are strongly developed between the veins, near the abaxial epidermis. In *C. angulare*, fibers are found between the veins, closer to the abaxial side of the duct.

Specimens seen: Panama, Cerro Jefe, *Dwyer et al. 7301*; *Mori & Kallunki 6503, 7301*; *Mori 7128* (all MO).

7. *Calophyllum rekoi* Standl., Contr. U.S. Natl. Herb. 20: 192. 1919. TYPE: Mexico, Oaxaca, *Reko 3557* (US). *Calophyllum brasiliense* var. *rekoi* (Standl.) Standl., Trop. Woods 30: 7. 1932. Figs. 6–7.

Midrib prominent, rounded or slightly 3-angled abaxially with a low rounded adaxial ridge. *Xylem* forms a narrow or broad V. Bundle angle 57–62° or 80–85°. *Sclerenchyma* forming 2 strands of fibers adaxial to the ends of the xylem trace,

the tissue between the two strands weakly lignified and in the Reko specimen lying against the adaxial ridge. *Secretory ducts* 1–5 in the ground tissue of the midrib.

LAMINA. *Adaxial epidermis* slightly thicker than the abaxial. *Veins* transcurrent, widely spaced. Frequency/height ratio 2–2.5:1. *Hypodermis* absent. *Palisade* cells in 2 layers occupying 40% of the mesophyll. *Secretory ducts* medium-sized, between the secondary veins and equidistant between the epidermal surfaces, not transcurrent or associated with sclerenchyma. *Druses* common in midrib ground tissue and in palisade and spongy mesophyll. *Sclereids* absent.

Much material collected in Central America has been determined as *C. rekoi* or as *C. brasiliense* var. *rekoi*, and these names have covered plants with small leaves as well as many with large leaves. The type collection has relatively large leaves, 12–14 cm long, 4–5 cm wide, superficially resembling those of *C. longifolium*, while the Calderón specimen has small leaves, 3.5–9 cm long, 2.5–3.5 cm wide, and seems representative of the relatively uniform small-leaved forms of Belize, Nicaragua, and El Salvador. It does not occur in Panama.

The two specimens examined differ very little. There is a slightly lower vein count in the Reko specimen. The shape of the midvein varies somewhat. There is more sclerenchyma beneath the adaxial surface of the midvein in the Reko specimen. It remains reasonable to associate them in a single variable species which differs notably from the other taxa studied in having a thin lamina and in having the lowest vein frequency/height ratio of the American species.

It is quite unreasonable to consider the Central American *C. rekoi* to be conspecific with the Brasilian *C. brasiliense*. Superficially, the specimens are different, *C. brasiliense* having subterete twigs while *C. rekoi* has notably angled twigs. *Calophyllum rekoi* has a hypodermis and the laminar ducts are only about half the size of those in *C. brasiliense*. It is unlikely that this species is conspecific with the type of *C. longifolium* and that *C. rekoi* should be placed into synonomy with the earlier *C. longifolium* (see discussion under *C. longifolium* above).

Specimens examined: Mexico, *Reko 3557* (US). El Salvador, *Calderón 147* (MO). Panama, *Dwyer 1670* (MO); *Holdridge 6232* (MO).

8. *Calophyllum soulattri* Burm. f., Fl. Ind. 2: 121. 1768. TYPE: Java, ?*Burman* (?G, not seen). *C. kunstleri* sensu auct., non King. FIG. 8.

MIDRIB prominent, rounded, slightly 2-angled abaxially with a low, rounded adaxial ridge. *Xylem* forms a wide rounded V. Bundle angle 70–75°. *Sclerenchyma* of fibers forming 2 strands adaxial to the ends of the xylem strand. There is weak lignification in the form of an inverted V of cells adjacent to the adaxial surface of the midrib. *Secretory ducts* small and frequent in the ground tissue of the midrib.

LAMINA. *Adaxial* and *abaxial epidermal* layers of equal thickness. *Veins* transcurrent, widely spaced. Frequency/height ratio 2.5–3:1. *Hypodermis* present. *Palisade* in 1(–2) layers occupying 25% of the mesophyll. *Secretory ducts* large, between the secondary veins and equidistant between the epidermal surfaces, surrounded by epithelium and by fibers with biseriate extensions, transcurrent and

strongly resembling secondary veins. *Druses* and *prismatic crystals* common in the ground tissue of the midrib, uncommon in the palisade layer. *Sclereids* absent.

Calophyllum soulattri has a high frequency/height ratio, but the hypodermis and transcurrent ducts in the lamina are reminiscent of *C. longifolium*. The duct diameter is smaller in *C. soulattri*, and its midrib is less strongly angular than *C. longifolium*. Otherwise, the two species are closer structurally than would be anticipated by their native ranges and floral characters. Our analysis reveals a species quite different from what Vesque (1889, 1893) described as *C. kunstleri* King.

This species is represented in Panama by several specimens collected early in this century from cultivation, and was listed, as *C. kunstleri*, in *Annual Reports of the Canal Zone Plant Introduction Gardens* (e.g., Johansen, 1926). The species is widespread in the Malaysian region. It is sometimes cultivated elsewhere (Stevens, pers. comm.) and it may be naturalized on Mauritius (Stevens, 1976). *Calophyllum soulattri* is distinct from all New World species of the genus in its small, glaucous fruits, only 11 mm across when mature (Stevens, 1976) and in its compound inflorescence which may appear subumbellate or fan shaped. Assistance from P. F. Stevens enabled us to determine our material of this species with confidence.

Unassignable Specimens

1. *Cooper & Slater 204* (MO, US). This sterile specimen has ovate leaves to 10 cm long and 4.5 cm wide, the apex is conspicuously acuminate and the base is obtuse. The veins are well spaced, ca. 16 per cm.

The label reads: Large forest tree over 75 ft × 24 inches; bark is rough and plated and when cut a sticky yellow sap exudes; wood is coarse, hard and used for general construction but not durable in contact with the ground. "Maria." Progreso, Chiriquí Province, 1927.

2. *Stern et al. 60* (MO, US). This sterile collection has ellipitical leaves to 13 cm long, 6 cm wide with blunt, obtuse and short acuminate tips and obtuse bases. They have dried partly yellowish and partly blackish and appear quite different from other Panamanian collections. The costa is contrasting. Except for the unusual coloration they appear much like *C. longifolium*.

The label reads: Tree 18 inches in diameter; bark with sticky yellow sap. "Maria." Foothills of Volcán Baru NW of El Hato, 4500 ft, Chiriquí Province, 6 June 1957.

Discussion

This study satisfied its basic goal of clarifying taxonomic relations between the main species of *Calophyllum* in Panama. From this work is became clear that neither *C. longifolium* nor *C. rekoi* can be justified as infraspecific taxa of *C. brasiliense*. Confidence could be attached to the placement of plants from other localities than Barro Colorado Island under *C. longifolium*, and recognition of the new species *C. nubicola* is now based on less subjective, superficial criteria than could otherwise have been noted. Of course, this is far short of what should

be done in preparing a revision of the New World or even Central American species of *Calophyllum*, for little extra-Panamanian material was examined. The full range of variability within a given taxon was only partly established. Extension of this study should produce useful results of application in other countries.

Our findings show that three native species of mainland America normally lack a hypodermis, while Vesque found hypodermis lacking in *C. calaba*. Clearly, a detailed study of New World *Calophyllum* is likely to produce an extended picture of the variability within the genus as a whole. For studies based on leaf histology, herbarium specimens are quite adequate since restoration is not a problem due to rigid support of the tissues by transcurrent veins and ducts. But while anatomical studies can provide valuable insights into systematic relationships and provide a check on variations in gross morphology, only study of many parts of the plants can support confident disposition of specimens into taxonomic groupings. Studies of living plants and of other features of the species will undoubtedly reveal many other characters of systematic importance in this taxonomically difficult genus.

A number of scatter diagrams were made in an attempt to detect clustering of characters or suggestions of trends which might be tested in future work. With one exception, almost no conclusions are possible with these data. The characters occur in almost any conceivable combination and appear to have been independently selected in each species. One would expect some correlation among functionally related features of leaf histology. The one trend noted is that vein frequency increases with lamina thickness.

The Old World species *C. inophyllum* and *C. soulattri* are not separable as a group from the New World species. *Calophyllum inophyllum* has an unusual midrib profile but its histological features are quite within the range of the other species examined.

An interesting phytogeographical comment concerns the close anatomical similarity between *C. longifolium* and the Old World introduction *C. soulattri*. One might have expected greater structural divergence based on geography, but perhaps various elements in the New World are more closely related to specific Old World taxa than others, and in some cases, the relationship might be quite close. We have not been able to explore this possibility and must advance it as speculation.

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MORTONIODENDRON (TILIACEAE) AND *SPHAEROPTERIS/TRICHIPTERIS* (CYATHEACEAE) IN CENOZOIC DEPOSITS OF THE GULF-CARIBBEAN REGION[1]

ALAN GRAHAM[2]

ABSTRACT

Two previously unidentified palynomorphs are common in Upper Tertiary deposits in the southern Gulf-Caribbean region. One is now identified as pollen of *Mortoniodendron* (Tiliaceae; Upper Miocene of Veracruz, Mexico, Middle Miocene of Panama, Pleistocene of Panama). The other represents spores of *Sphaeropteris/Trichipteris* (Cyatheaceae; Upper Miocene of Veracruz, Mexico). Neither have previously been reported in the fossil record.

For a number of years two very distinct, unidentified palynomorphs have been known from Cenozoic deposits in the southern Gulf-Caribbean region. One of these is a relatively small, oblate, tricolpate, finely reticulate pollen grain with conspicuous endexine thickenings about the shortened colpus (costae colpi). The other is a trilete spore with numerous conspicuous pits in the wall. The biological affinities of the microfossils were unknown, but considering the relatively recent age of the specimens and their distinctive morphology, it seemed likely identifications would eventually be made. Both microfossils have now been identified, and they represent genera previously unreported in the fossil record.

MORTONIODENDRON (Tiliaceae)

Pollen description (fossil).—Peroblate, oval-triangular in polar view; tricolpate, the colpi equatorially arranged, meridionally elongated, equidistant, the inner margin entire, short (ca. 3.5 μm apex to equator), conspicuous costae colpi ca. 1.5–2 μm wide; semitectate; finely to moderately reticulate (diameter of the lumen from ca. 1 μm to 3 μm at the poles, finer toward the equator), reticulum closed, regular, the muri ca. 0.5 μm wide, straight to occasionally slightly sinuous, the surface psilate, the margins entire; size 18–27 μm.

This pollen type was recovered from the Upper Miocene Paraje Solo Formation, exposed in southeastern Veracruz state near the port of Coatzacoalcos, Mexico (Graham, 1976: 840, figs. 248–255; Fig. 3, this report). Later specimens were also found in core material from Gatun Lake, Canal Zone, Panama (Fig. 2). These sediments are from the Gatun Formation and are Middle Miocene in age. Bartlett & Barghoorn (1973: 242) reported similar specimens from Pleistocene deposits of the Canal Zone and suggested they may represent *Mortoniodendron*, although reference material was not available to them. The specimens have long been thought to represent some member of the Tiliaceae, or possibly the Stercu-

[1] I gratefully acknowledge reference pollen material and information on *Mortoniodendron* provided by Lorin Nevling (Field Museum). Gerald Gastony (Indiana University) provided spore material of *Sphaeropteris* and *Trichipteris*, as well as the SEM photomicrograph of *Sphaeropteris*, and his help and suggestions are sincerely appreciated.

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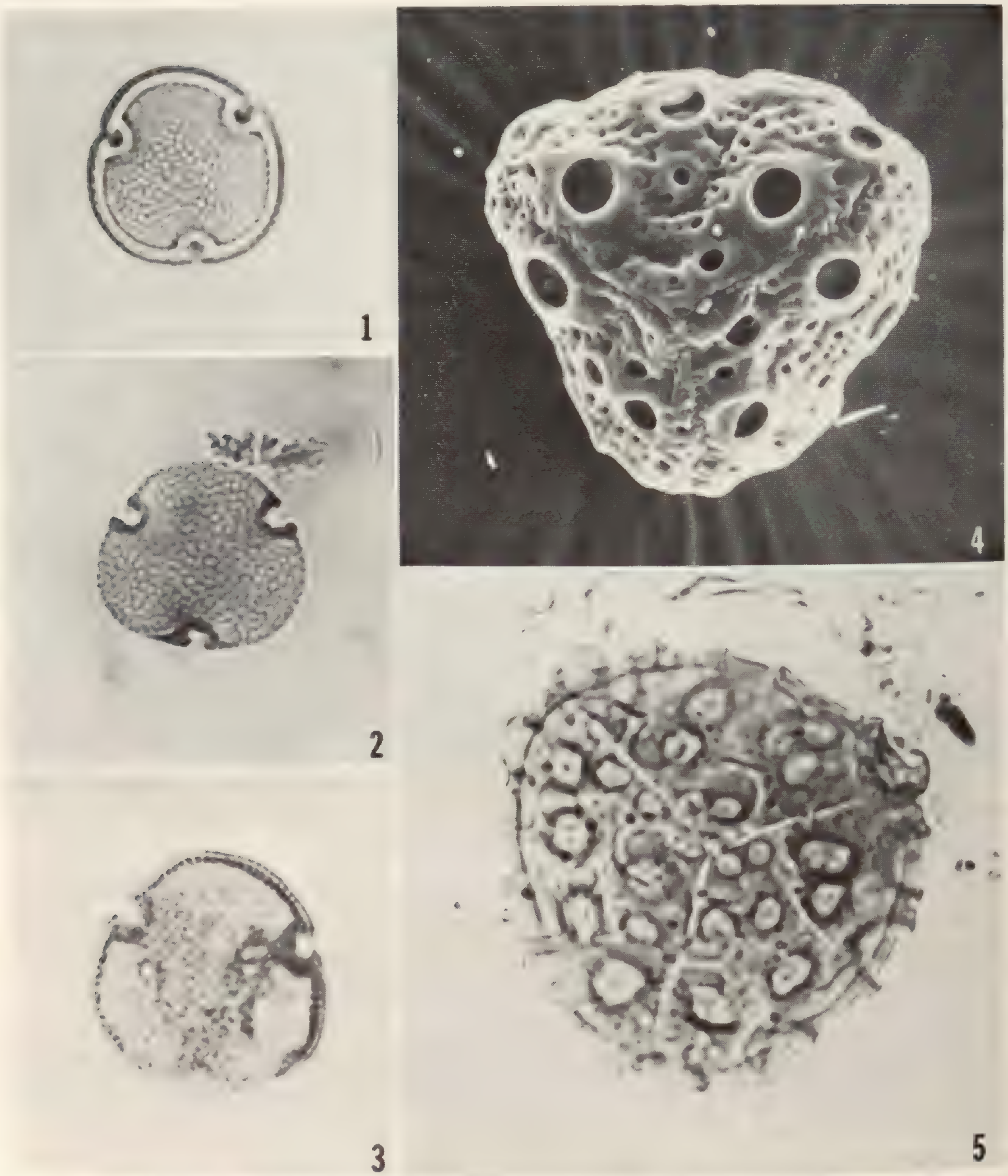
liaceae, because of the distinctive thickenings about the shortened colpi, as occur in *Tilia*. The principal difference between the fossil specimens and pollen of *Tilia* is that the fossil grains are only about half the size (ca. 18–27 μm vs. 40–50 μm). Limited amounts of flowering material of two species (*M. guatemalense* Standley & Steyermark, Fig. 1; *M. membranaceum* Standley & Steyermark) were obtained from the Field Museum (Nevling, pers. comm., 1976), and the fossil specimens can now be referred to *Mortoniodendron*.

The genus consists of about five species distributed from Mexico (states of Chiapas, Veracruz) through Central America. The plants range from small shrubs ca. 1 m tall (*M. hirsutum* Standley, Panama; *M. membranaceum* Standley & Steyermark, Honduras) to tall tropical forest trees (*M. anisophyllum* (Standley) Standley & Steyermark, Costa Rica, Panama). In Costa Rica the genus is represented in the lowlands of the Golfo Dulce by *M. anisophyllum* and *M. guatemalense* var. *australe* Morton & Steyermark. There the former species includes trees up to 30 m tall, and with the larger specimens strongly buttressed. In Veracruz *M. guatemalense* occurs in the Selva Alta Perennifolia (high evergreen selva, tropical rain forest) associated with *Terminalia amazonia* (Gmell.) Exell, *Calophyllum brasiliense* Camb., *Dialium guianense* (Aubl.) Sandwith, *Bernoullia flammea* Oliver, *Brosimum alicastrum* Sandwith, *Ficus tecolutensis* (Liebm.) Miq., and *Pseudolmedia oxyphyllaria* Donn.-Smith as dominants. Other aspects of the distribution and ecology of *Mortoniodendron* have been noted by Allen (1956: 268–269), Gómez-Pompa (1973: 108, 111), and Robyns (1964: 15–18). The genus is poorly known taxonomically and individual species are rarely represented by both flowering and fruiting herbarium material; Robyns (Paris) is presently preparing a monograph of *Mortoniodendron*.

There have been too few studies in neotropical Cenozoic paleobotany to accurately summarize the probable stratigraphic range and paleogeographic distribution of *Mortoniodendron*. It is present in the Middle Miocene Gatun Formation of the Canal Zone, the Upper Miocene Paraje Solo Formation of Veracruz, Mexico, and in the Pleistocene Gatun Lake deposits of the Canal Zone; all are within the present range of *Mortoniodendron*. It has not been recovered from palynofloras studied from the lower Middle Eocene Chapelton Formation of Jamaica (Graham, 1977; unpubl. data), the Oligo-Miocene Simojovel Group of Chiapas, Mexico (Langenheim et al., 1967), the Oligocene San Sebastian Formation of Puerto Rico (Graham & Jarzen, 1969) or from the several Eocene to Oligo-Miocene microfloras presently under study from Panama (Graham, unpubl. data). It is not mentioned in Germeraad et al.'s extensive 1968 summary of Tertiary palynology of South America. To my knowledge it has not been reported from either the modern or fossil floras of South America, nor is it presently known from the megafossil record. Thus on the basis of information currently available, *Mortoniodendron* ranges from Middle Miocene to Recent, based on three known occurrences in southern Mexico and the Canal Zone.

SPHAEROPTERIS/TRICHIPTERIS (Cyatheaceae)

Spore description (fossil).—Radially symmetrical, the amb oval-triangular, the margin lobate (from pits in equatorial section); trilete, the arms straight,



FIGURES 1–5.—1. Modern pollen of *Mortoniodendron*, ca. 20 μm.—2. Fossil pollen of *Mortoniodendron*, Gatun Formation, Panama, core SL 103, Harvard University No. 31, 253′ depth, slide No. 3, England Slide Finder Coordinates D-47, 3,4, ca. 22 μm.—3. Fossil pollen of *Mortoniodendron*, Paraje Solo Formation, Veracruz, Mexico, slide 34-1, ESF coordinates L-30, 1–3, 27 μm.—4. SEM photomicrograph of spore of modern *Sphaeropteris myosuroides*, ca. 55 μm.—5. Fossil spore of *Sphaeropteris/Trichipteris*, Paraje Solo Formation, Veracruz, Mexico, slide 10-1, ESF coordinates C-45, 65 μm.

narrow, the margins entire, ca. 18 μm long, extending ca. ⅔ the distance from the pole to the equator; wall conspicuously pitted, the pits circular, 1.5–4 μm diameter, the inner margin entire, the raised border ca. 1.5 μm wide, irregularly distributed; size ca. 55 μm.

The distinctive feature of these spores is the conspicuous pits in the wall

(Fig. 5). Initially it was thought these were made by chytridiaceous phycomycete fungi, or were imprints of mineral crystals. Both conditions are occasionally observed on fossil pollen and spores. Photographs were circulated among palynologists and similar opinions were expressed. This view was supported by the irregular distribution of the pits over the spore surface. Later, however, additional specimens were recovered and it seemed more likely the pits were a natural feature of the spore ornamentation. It was further assumed that the spores probably represented some member of the Cyatheaceae because somewhat similar pits occur in *Hemitelia* (*Cnemidaria*).

In 1976 Gastony and Tryon published a paper on the spore morphology of the Cyatheaceae, which included photographs of *Sphaeropteris*. These spores (especially their fig. 65) were very similar to the fossil specimens recovered from the Upper Miocene Paraje Solo Formation of Veracruz, Mexico. In addition to *S. myosuroides* (Liebm.) Tryon (Fig. 4), however, Gastony (pers. comm., 1976) also provided spore material of *Trichipteris mexicana* (Mart.) Tryon which were also similar. The fossil specimens resembled most closely those of *Sphaeropteris*, based on minor quantitative differences, but since no consistent distinguishing feature could be found, the spores are identified as *Sphaeropteris/Trichipteris*.

Both *Sphaeropteris* and *Trichipteris* are tree fern genera presently occurring in the modern vegetation of Veracruz. *Sphaeropteris myosuroides* is a lowland species of the tropical rain forest, but ranges into more temperate communities (Gómez-Pompa, 1973: 110). It occurs in Cuba and from Mexico south to Nicaragua at elevations from ca. 10 to 600 m. *Trichipteris mexicana*[3] occurs from Mexico to Honduras in the tropical rain forest, cloud forest, and along waterways, but grows at higher elevations (800–3,000 m). Since the microfossils are preserved in lignites, deposited under lowland, coastal conditions, ecological considerations would favor *Sphaeropteris* entering this depositional environment.

Another species, *Trichipteris microdonta* is also widespread from northern Latin America into South America and occurs from sea level to 1,700 m, including one report from brackish coastal waters in Nicaragua (Barrington, 1978). However, the spores of this species have a perine of hairlike processes covering an exine which is strongly but finely pitted on both the proximal and distal faces (Gastony, pers. comm., 1978), and thus are quite different from the fossil specimens.

To my knowledge spores of *Sphaeropteris/Trichipteris* are presently known only from the Paraje Solo Formation, and the genera have not been reported in the megafossil record. Other information on ecology and distribution are given by Windisch (1977) and Barrington (1978).

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[3] Corrected name of *T. bicrenata* in Gastony & Tryon (1976; Gastony, pers. comm., 1976).

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ADDENDUM: In galley a paper by Tschudy and van Loenen (1970, U.S. Geol. Surv. Prof. Paper 643-E, Figs. 11a,b, 14, 15) was found reporting specimens similar to *Mortoniodendron* from the Upper Eocene of Mississippi under the name *Tiliaepollenites*. This extends the geographic range to Mississippi and the stratigraphic distribution from Upper Eocene to Present.

CHROMOSOME NUMBERS AND RELATIONSHIPS OF CERTAIN AFRICAN AND AMERICAN GENERA OF HAEMODORACEAE[1]

ROBERT ORNDUFF[2]

ABSTRACT

Chromosome numbers of $n = 15$ are reported for *Barberetta aurea*, *Wachendorfia paniculata*, and *W. thyrsiflora*; $n =$ ca. 19–21 for *Dilatris pillansii*; $n = 24$ for *Lachnanthes caroliniana*; $n = 21$ for *Lophiola aurea*; and $n = 36$ for *Lanaria plumosa*, a genus of uncertain familial position sometimes assigned to Haemodoraceae. *Barberetta* and *Wachendorfia* are believed to be closely related, but the relationships of the other genera are unclear and indicate that further detailed study is merited.

The family Haemodoraceae has been variously circumscribed by different authors. A recent detailed study of familial limits recognized 14 genera (Geerinck, 1969; but see de Vos, 1956, and Hutchinson, 1973). The tribe Conostylideae contains the Australian genera *Anigozanthos*, *Conostylis*, and *Tribonanthes*. The tribe Haemodoreae contains the Australasian-Oceanic genera *Haemodorum* and *Phlebocarya*; the New World genera *Lophiola*, *Lachnanthes*, *Schiekia*, *Pyrrorhiza*, *Hagenbackia*, and *Xiphidium*; and the South African *Barberetta*, *Dilatris*, and *Wachendorfia*. The New World genera are monotypic; only *Barberetta* of the Old World genera is monotypic, with the others containing a few to many species. In South Africa, *Wachendorfia* is particularly variable and is in need of systematic study. Although chromosome counts are available for several species of the Conostylideae (Green, 1960), only a single chromosome count has been published for the considerably larger and more widespread Haemodoreae. This paper presents chromosome counts of two New World and three South African genera of Haemodoraceae. Because *Lanaria* has on occasion been referred to the Haemodoraceae, a chromosome count for it is also included here.

MATERIALS AND METHODS

During 1970–1971, living material or flower buds of various Haemodoraceae were collected by the author in South Africa and sent to the Botanical Garden of the University of California, Berkeley, where additional cytological material was obtained from cultivated specimens for microscopic study. North American Haemodoraceae were provided by R. K. Godfrey, grown at Berkeley, and preparations made from these plants for observation of microsporogenesis.

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[1] I am grateful to the staffs of the Compton and Bolus herbaria for their hospitality during my stay in South Africa; the National Science Foundation, Bache Fund of the National Academy of Sciences, and C.S.I.R. (South Africa) for financial assistance; Mrs. Patricia Watters for technical assistance; Dr. Peter Goldblatt for helpful comments on the manuscript; and Dr. R. K. Godfrey for providing plants collected in Florida.

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TABLE 1. Chromosome numbers of Haemodoraceae. All localities for South African taxa are in the Cape Province. Collection numbers without name are the author's.

Taxon	Chromosome Number (n)	Locality
Barberetta aurea Harv.	15	Between Blinkwater and York, Natal: *7661.*
Dilatris pillansii Barker	ca. 19–21	Cape Point Nature Reserve: *7647.*
Lachnanthes caroliniana (Lam.) Dandy	24	Lanark Village, Franklin Co., Florida: *Godfrey 70922.*
Lanaria plumosa Ait.	36	Nr. Elgin: *7702.*
Lophiola aurea Ker-Gawl.	21	Nr. Sumatra, Liberty Co., Florida: *Godfrey 70990.*
Wachendorfia paniculata Burm. sens. lat.	15	Kapteinskloof: *7134.*
	15	Darling Reserve: *7162.*
	15	Kenilworth: *7268.*
	15	Mamre: *7308*
	15	Clanwilliam: *7409.*
	15	Nieuwoudtville: *7452.*
Wachendorfia thyrsiflora Burm.	ca. 15	Kirstenbosch: *7612.*
	ca. 15	Grabouw/Villiersdorp: *7615.*

RESULTS

Thirteen collections were examined of six species of Haemodoraceae and of *Lanaria plumosa*. Chromosome numbers of $n = 15$, ca. 15, ca. 19–21, 21, and 24 were obtained for the Haemodoraceae; $n = 36$ for *L. plumosa* (Table 1).

DISCUSSION

The only chromosome count previously reported for a member of the Haemodoreae is $n = 15$ for *Barberetta aurea* (Hilliard & Burtt, 1971). The few species of the Conostylideae examined have $n = 4, 5, 7, 8, 14$ (*Conostylis*) and 6 (*Anigozanthos*; Green, 1960). My count of $n = 15$ for *Barberetta aurea* confirms the earlier one and was obtained from plants collected in a locality different from that in which the plants studied by Hilliard and Burtt originated. *Barberetta* is, in my opinion, much more closely related to *Wachendorfia* than to *Dilatris*. *Barberetta* and *Wachendorfia* both have plicate leaves, orange flowers, enantiostyly, pigmented corms, and other morphological characters in common. This presumed relationship is further borne out by the occurrence of $n = 15$ in the two species of *Wachendorfia* examined. The collections attributed to *W. paniculata* are variable in a number of characteristics. It is possible that further study of *W. paniculata* sensu lato and its allies will result in the description of additional species.

The approximate count of $n = 19$–21 for *Dilatris pillansii* is dissimilar to the counts of $n = 15$ for *Wachendorfia* and *Barberetta*, genera that it also does not resemble closely in morphological characters. Robertson (1976) concluded that there is a close relationship between *Dilatris* and *Lachnanthes*. In overall vegetative aspect and in certain details of the inflorescence, the two genera are similar. Their probable close relationship is further supported by the occurrence of $n = 24$ in *Lachnanthes*, which, while not identical to the $n = 19$–21 recorded for *Dilatris pillansii*, is also clearly not based on the $x = 15$ of *Barberetta* and *Wachendorfia*. However, de Vos (1956), on the basis of embryological characters, concluded that *Wachendorfia* and *Dilatris* are rather closely related to each other, as well as to *Xiphidium* and *Anigonzanthos*.

The taxonomic position and relationships of *Lophiola* have been the subject of disagreement among various workers. Hutchinson (1973) placed the genus in the Conostylideae; Geerinck (1969) placed it in the Haemodoreae next to *Lachnanthes*. Robertson (1976) stated that *Lophiola* has little in common with other members of the Conostylideae but also said that despite the superficial similarities between *Lophiola* and *Lachnanthes*, the differences between them are numerous and "it seems doubtful" that they are related. The chromosome number of $n = 21$ for *Lophiola* would suggest a possible close relationship to *Dilatris* and perhaps even *Lachnanthes*, and a more distant relationship to *Wachendorfia* and *Barberetta*. On the basis of gross morphology and chromosome number, *Lophiola* seems more at home in the Haemodoreae than in the Conostylideae. De Vos (1963) has pointed out several anatomical and palynological similarities between *Lophiola* and *Lanaria*. The latter genus has been variously placed in Haemodoraceae, Liliaceae, and Tecophilaeaceae (Airy Shaw, 1973; Robertson, 1976). Its chromosome number of $n = 36$ does not clearly aid in supporting any of these familial assignments, although $n = 12$ is present in three genera of Tecophilaeaceae, including *Cyanella* of South Africa (Ornduff, 1979). However, $x = 6$ for the Australian haemodoraceous genus *Anigozanthos* as well (Green, 1960). On embryological grounds, de Vos (1961, 1963) suggested that *Lanaria* has a closer relationship with genera of the Tecophilaeaceae than with the Haemodoraceae, although she did not rule out possible relationship to certain genera of Liliaceae and Amaryllidaceae. The substantial and continuing disagreements concerning the limits of the Haemodoraceae and the relationships of the genera assigned to it indicate that the family merits additional detailed study.

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CHROMOSOME NUMBERS IN *CYANELLA* (TECOPHILAEACEAE)[1]

ROBERT ORNDUFF[2]

ABSTRACT

Chromosome numbers are reported for the four species of *Cyanella* that occur in South Africa. Seven collections of *C. hyacinthoides* had $n = 12$, five had $n = 24$, and one had $n = 14$. Two collections of *C. alba* had $n = 12$. One collection of *C. orchidiformis* had $n = 12$. Four collections of *C. lutea* had $n = 12$, two had $n = 24$, an unusual color variant had $n = 8$. Three other genera of the family are recorded as having $n = 10$, $n = 11$, 12, and $n = 12$, respectively. It is likely that $x = 12$ for the family and that other numbers represent examples of aneuploid increase or reduction from this base number.

Cyanella is a small genus of six to eight species found in the Cape Province of South Africa and in adjacent South West Africa (Namibia). Placement of the genus has been a matter of some dispute, though current opinion puts it in the small family Tecophilaeaceae (sensu Airy Shaw, 1973) comprising six genera, each with one or a few species. Three of these genera—*Tecophilaea*, *Conanthera*, and *Zephyra*—are restricted to Chile, *Odontostomum* is endemic to California, and *Cyanastrum* occurs in tropical Africa. Chromosome counts have been reported for single species each of *Cyanastrum* ($n = 11$, Satô, 1942; $n = 12$, Nietsch, 1941), *Tecophilaea* ($n = 12$, LaCour, 1956), and *Odontostomum* ($n = 10$, Cave, 1949). No chromosome numbers have been reported for the remaining three genera. This paper presents a chromosomal survey of the four species of *Cyanella* that occur in South Africa; Mauve (pers. comm.) regards *C. pentheri* Zahlbr. as synonymous with *C. hyacinthoides* L.

MATERIALS AND METHODS

During 1970–1971 living specimens of *Cyanella* were collected in the Cape Province and sent to the University of California Botanical Garden (Berkeley). When planted specimens flowered, anthers were removed, fixed, and squashed in aceto-carmine for examination of microsporogenesis.

RESULTS

Twenty-three collections of four species were examined. Chromosome numbers of $n = 8$, 12, 14, and 24 were obtained (Table 1).

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[1] I am indebted to Mrs. A. A. (Obermeyer) Mauve for assistance with nomenclature; Dr. Peter Goldblatt for helpful comments on the manuscript; the staffs of the Compton Herbarium and the Bolus Herbarium for their hospitality during my stay in South Africa; the National Science Foundation, the Bache Fund of the National Academy of Sciences, and the C.S.I.R. (South Africa) for financial assistance; Mr. and Mrs. Neal McGregor of Glenlyon Farm for assistance in locating an unusual color variant of *C. hyacinthoides*; and Mrs. Patricia Watters for technical assistance.

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TABLE 1. Chromosome numbers in *Cyanella*. Collection numbers are the author's. All localities are in the Cape Province, South Africa.

Taxon	Chromosome Number (n)	Locality
Cyanella alba L.f.	12	Bidouw Valley: *7424*.
Cyanella hyacinthoides L.	24	3 mi N of Citrusdal: *7399*.
	24	Btw. Citrusdal and Clanwilliam: *7403*.
	12	4 mi W of Clanwilliam: *7412*.
	12	1.5 mi W of Clanwilliam: *7416*.
	12	Doringbos: *7420*.
	12	Near Doringbos: *7425*.
	12	Bulshoek Dam: *7440*.
	12	Klipkoppies, Nieuwoudtville: *7457*.
	12	Bidouw Valley: *7475*.
	24	1 mi W of Clanwilliam: *7481*.
	14	Bainskloof: *7501*.
	24	Modderrivier, near Darling: *7526*.
	24	Kirstenbosch (native): *7632*.
Cyanella lutea L.f. var. *lutea*	ca. 12	Worcester: *7355*.
	24	Swartberg Pass: *7561*.
	24	Swartberg Pass: *7565*.
	12[a]	11 mi E of Avontuur: *7598*.
	12	24 mi W of Knysna: *7655*.
	8	Tygerberg: *7697*.
Cyanella lutea L.f. var. *rosea* Bak.	12	White's Farm, Grahamstown: *7658*.
Cyanella orchidiformis Jacq.	12	Nuwerus: *7187*.

[a] With laggards.

DISCUSSION

The most widely sampled species was *Cyanella hyacinthoides*, of which thirteen collections were examined. Seven of these had $n = 12$, including an unusual orange-flowered variant (*7457*) from the vicinity of Nieuwoudtville. One collection (*7501*) from Bainskloof had $n = 14$; whether this number is typical for the population is uncertain. Five collections had $n = 24$ and are probably tetraploid based on $n = 12$. There are no obvious morphological or distributional traits that separate the diploid and tetraploid races of *C. hyacinthoides*. Both occur very near each other in the vicinity of Clanwilliam. The two collections examined of *C. alba* L.f. both had $n = 12$; these included a color variant (*7463*) that possessed tepals with dark maroon lower surfaces. The single collection of

C. orchidiformis Jacq. likewise had $n = 12$. *Cyanella lutea* L.f. is chromosomally as well as morphologically variable. Chromosome numbers of $n = 8$, 12, and 24 were obtained for *C. lutea* var. *lutea*. An unusual color variant from the Tygerberg (*7697*), with gold rather than lemon yellow flowers, had $n = 8$, the only known occurrence of this chromosome number in the genus. The single collection examined of *C. lutea* var. *rosea* had $n = 12$.

The relationships of *Cyanella* to other genera of the family are unclear. Hutchinson (1973) considered that "*Cyanastrum* is undoubtedly closely allied to *Cyanella*." Although $n = 12$ (as well as $n = 11$) has been reported for *Cyanastrum*, the two genera are very dissimilar morphologically and cannot be considered closely related. Sterling (1974) concluded that *Cyanella* is closely related to the African genus *Walleria* (and, by implication, to *Tecophilaea*), a genus referred to the Tecophilaeaceae by Hutchinson (1973, although he also has it listed in brackets in the Liliaceae-Dianelleae) but by Airy Shaw (1973) to the Liliaceae.

Thus, in the Tecophilaeaceae, chromosome numbers of $n = 8$, 10, 11, 12, 14, and 24 are known. The occurrence of $n = 12$ in three genera suggests the possibility that $x = 12$ is a common base number for the family, with $n = 24$ representing a tetraploid chromosome number. The sequence $n = 8$, 10, and 11 thus may represent a decreasing aneuploid series and $n = 14$ an example of aneuploid increase above the base number of 12.

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CHROMOSOME NUMBERS OF FOUR SPECIES OF *DROSERA* (DROSERACEAE)[1]

KATSUHIKO KONDO[2] AND M. C. OLIVIER[3]

ABSTRACT

Chromosome numbers of four species of *Drosera* are newly reported. Chromosome counts for *D. cistiflora* ($2n = 40$), *D. glanduligera* ($2n = 22$), and *D. nitidula* ($2n = 28$) contribute toward a determination of new basic chromosome numbers for sects. *Ptycnostigma* ($x = 10$), *Coelophylla* ($x = 11$), and *Lamprolepis* ($x = 11$), respectively. The count of $2n = 30$ for *D. schizandra* verifies the basic number previously reported for sect. *Arachnopus*.

Chromosome numbers of various *Drosera* taxa have been reviewed and reported by Kondo (1966, 1969, 1970, 1971a, 1971b, 1973, 1976), Kondo & Whitehead (1971), and Kondo, Segawa & Nehira (1976). Since chromosome counts are of great biosystematic importance in *Drosera*, additional reports of chromosome numbers are useful and should contribute to a better understanding of the genus.

MATERIALS AND METHODS

Materials used in this study were collected from the following sources:

Drosera cistiflora L. Ca. 11 km west of the center of Port Elizabeth, Republic of South Africa, south of the road leading to Humansdorp. Voucher specimen: *Olivier 1948*; deposited in the Herbarium, The University of Port Elizabeth (UPE).

Drosera glanduligera Lehm. Western Australia, Australia (collected by W. J. Forrest, Te Puke, New Zealand). Voucher specimen: *Forrest s.n.*; deposited in the Herbarium, Faculty of Integrated Arts and Sciences, Hiroshima University (*Kondo 1805*).

Drosera nitidula Planch. Native to Western Australia, Australia (exact source unknown; cultivated by M. Hirano, Tokyo, Japan). Voucher specimen: *Hirano s.n.*; deposited in the Herbarium, Faculty of Integrated Arts and Sciences, Hiroshima University (*Kondo 1806*).

Drosera schizandra Diels. Native to Queensland, Australia (exact source unknown; cultivated by M. Hirano, Tokyo, Japan). Voucher specimen: *Hirano s.n.*; deposited in the Herbarium, Faculty of Integrated Arts and Sciences, Hiroshima University (*Kondo 1807*).

Somatic chromosomes at midmetaphase were obtained from apical cells of shoots of the above mentioned clones. The shoot apices were treated with 0.002M hydroxyquinoline at 18°C for four hours before they were fixed in Carnoy's solution (95% ethanol:chloroform:glacial acetic acid in a ratio of 2:1:1) at 4°C, following which they were hydrolyzed and stained in a 10:1 mixture of 2% aceto-orcein and 1 N-hydrochloric acid at room temperature (ca. 20°C) for 30 minutes, and then squashed in 2% aceto-orcein.

RESULTS AND DISCUSSION

Drosera cistiflora has a somatic chromosome number of $2n = 40$ (Figs. 1–2). This chromosome number is different from that previously reported by Behre

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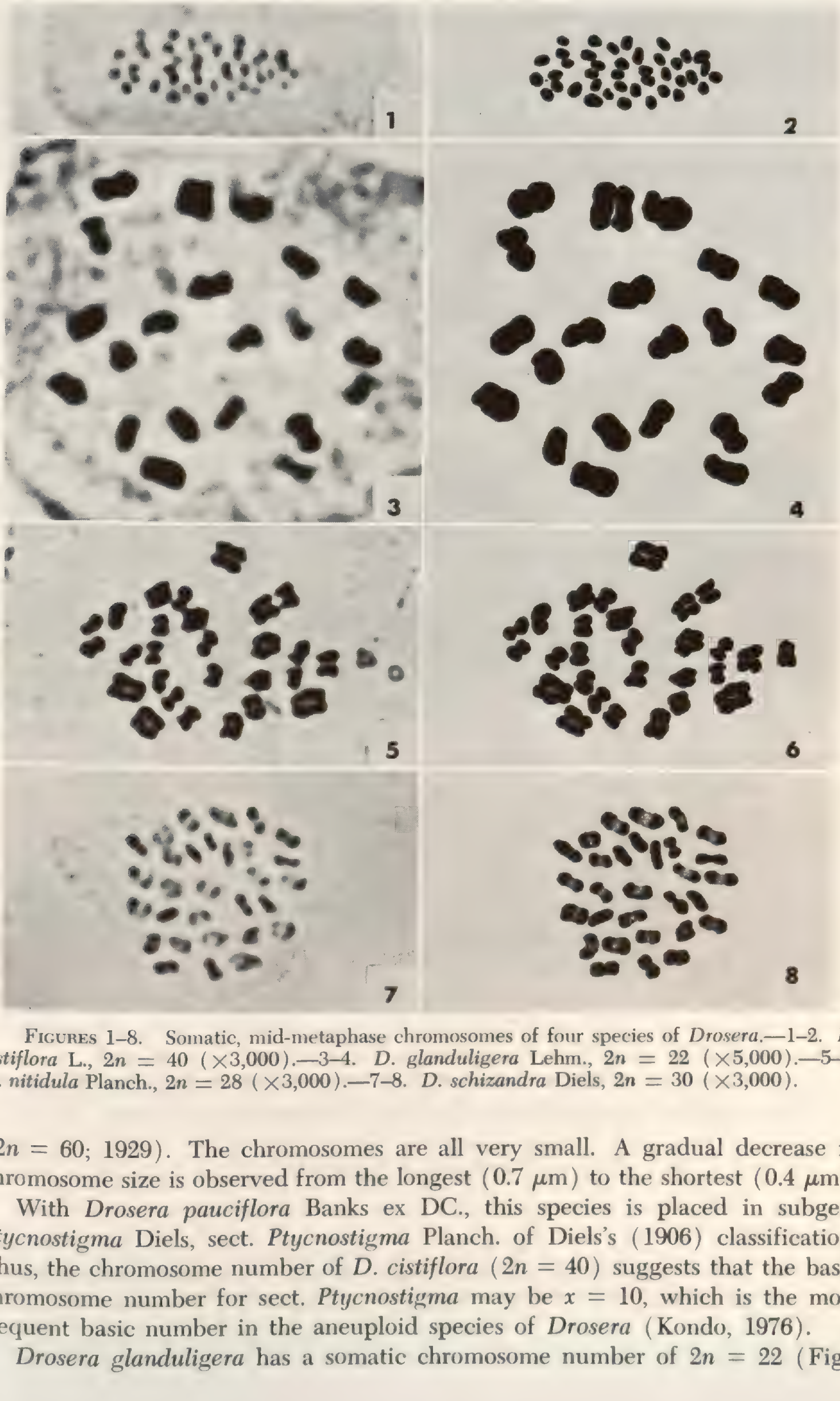

FIGURES 1–8. Somatic, mid-metaphase chromosomes of four species of *Drosera*.—1–2. *D. cistiflora* L., $2n = 40$ (×3,000).—3–4. *D. glanduligera* Lehm., $2n = 22$ (×5,000).—5–6. *D. nitidula* Planch., $2n = 28$ (×3,000).—7–8. *D. schizandra* Diels, $2n = 30$ (×3,000).

($2n = 60$; 1929). The chromosomes are all very small. A gradual decrease in chromosome size is observed from the longest (0.7 μm) to the shortest (0.4 μm).

With *Drosera pauciflora* Banks ex DC., this species is placed in subgen. *Ptycnostigma* Diels, sect. *Ptycnostigma* Planch. of Diels's (1906) classification. Thus, the chromosome number of *D. cistiflora* ($2n = 40$) suggests that the basic chromosome number for sect. *Ptycnostigma* may be $x = 10$, which is the most frequent basic number in the aneuploid species of *Drosera* (Kondo, 1976).

Drosera glanduligera has a somatic chromosome number of $2n = 22$ (Figs.

3–4). The chromosomes are small and similar to each other in shape. The longest (1.3 μm) and shortest chromosomes (1.1 μm) are roughly the same size. Since this is the only species in subgen. *Rorella* DC., sect. *Coelophylla* Planch., the chromosome number of this species indicates that the basic chromosome number for the section is $x = 11$. This basic chromosome number is new in the genus and it in part bridges the gap between two previously known basic numbers, i.e., $x = 10$ and $x = 13$.

Drosera nitidula has a somatic chromosome number of $2n = 28$ (Figs. 5–6). The chromosomes are distributed in two size classes, one with eight large chromosomes (ave. 1.7 μm) and another with 20 short chromosomes (ave. 0.7 μm in size). *Drosera nitidula* is placed in subgen. *Rorella*, sect. *Lamprolepis* Planch., in which the reported basic chromosome number is $x = 9$ (Kondo, Segawa & Nehira, 1976). Thus, the chromosome number $2n = 28$ and the basic chromosome number $x = 7$ or 14 found in *D. nitidula* are new to the section, but are the same as those in the related sect. *Bryastrum* Planch., which has a single species, *D. pygmaea* DC. (Kondo, Segawa & Nehira, 1976). Members of sections *Lamprolepis* and *Bryastrum* have chromosomes exhibiting similar morphological patterns, as well as similarities in leaf morphology and asexual reproduction.

The nonstaining gap between the chromatids of each chromosome is rather wide and the centromeric region is not clearly seen throughout prophase, prometaphase, and midmetaphase. This may be a cause of polycentric chromosomes which lack a single, localized centromere (Kondo, Segawa & Nehira, 1976).

Drosera schizandra has a somatic chromosome number of $2n = 30$ (Figs. 7–8). All the chromosomes are small (ave. 1.1 μm in size) and similar to each other in shape. Midmetaphase chromosomes have well-stained distal segments and poorly stained proximal segments (Figs. 7–8). This species is placed in subgen. *Rorella*, sect. *Arachnopus* Planch. with two other species, *D. adelae* F. Muell. and *D. indica* L. *Drosera schizandra* and *D. adelae* both have the somatic chromosome number of $2n = 30$, although the latter species has another cytotype with $2n = 28$ in a cultivated population (Kondo, 1976; Kondo, Segawa & Nehira, 1976). *Drosera indica* shows $2n = 28$ (Venkatasubban, 1950; Kondo, 1966).

The results of this study provide new data for representative species of those sections of *Drosera* in which basic chromosome numbers were previously unknown. With the new basic chromosome number $x = 11$ from *Drosera glanduligera*, members of *Drosera* thus far studied cytologically form an aneuploid series with basic chromosome numbers of 6, 7, 8, 9, 10, 11, 13, and 14.

Further cytological observations of other species of *Drosera* should improve our concept of the interrelationships between the species of *Drosera*.

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THE *HOMERIA* SPECIES OF THUNBERG'S HERBARIUM[1]

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ABSTRACT

Thunberg's South African collections contain the type material for four species which conform to current concepts of *Homeria*. A detailed examination of the type material in the Thunberg Herbarium has resulted in selection of lectotypes for three of these species, where more than one sheet of a species was present. *Homeria collina* (Thunb.) Vent and *H. umbellata* (Thunb.) Lewis remain as presently interpreted. However, the name *Moraea polyanthos* L.f., as currently understood is misapplied and is an earlier name for *H. lilacina* L. Bol. The species at present called *M. polyanthos* now becomes *M. bipartita* L. Bol. The type of the fourth species, *M. crispa*, is incomplete, but it is very likely that it is simply a crisped-leafed form of the widespread Karoo species *H. rogersii* L. Bol. for which it is an earlier synonym. No new combinations in *Homeria* are made here. The genus is currently under investigation, and the definition of *Homeria* and the related *Moraea* is being revised.

Homeria is a genus of some 30 species of Iridaceae-Irideae, endemic in southern Africa. Species are concentrated in the Cape Region of South Africa, and, where they occur, are generally very common plants. Strangely, Thunberg's collection from the Cape, now housed in the herbarium of the Institute for Systematic Botany, University of Uppsala, Sweden, has few specimens of the genus, and from these only four species were described. This is most likely because Thunberg thought there were only a few species where today we recognize many, and so he collected no more specimens once he felt he had gathered the basic types.

Thunberg, and as well the younger Linnaeus, who worked on Thunberg's collections, considered *Homeria* indistinguishable from genera such as *Aristea*, *Ferraria*, *Tigridia*, and *Bobartia*, and they placed species of all these genera in *Moraea*. True species of *Moraea* they regarded as *Iris*, and Thunberg collected a large number of species of true *Moraea*, a very variable genus at the Cape.

Of the many species of "*Moraea*" which Linnaeus fil. and Thunberg described, the following four are *Homeria*-like. The first is *M. polyanthos* L.f. (1781); followed by *M. collina*, *M. umbellata* and *M. crispa*, all described by Thunberg (1787).

In modern times, N. E. Brown (1928) examined Thunberg's Iridaceae, including the few *Homeria* species. I have recently examined the specimens in question, not always agreeing with Brown's conclusions. The sheets are listed below by species with the numbers assigned to them on the microfiche of Thunberg's herbarium.

1. *Moraea collina* Thunb.

   1209 Specimen has a large pale flower; anthers 7 mm long, slightly diverging; tepals ca. 40 mm long, 15 mm wide; ovary 12 mm long. A good match for the common Cape Peninsula species now known as *H. collina* (Thunb.) Salisb. ***This specimen is the lectotype.***

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1210 Probably also *H. collina* but less well preserved, possibly a related species.

1211 This is a very tall, single-leafed plant, the leaf sheathing the lower part of the stem, which is much branched: probably what is currently called *H. pillansii* L. Bol. (It is not *Moraea gigantea* as suggested by Brown, this being a synonym of *H. miniata.*)

1212 Specimen has three leaves, is short in stature and is in fruit: probably *H. miniata* (Andr.) Sweet.

2. *M. umbellata* Thunb.

1230 This is the Cape plant currently called *H. umbellata* (Thunb.) Lewis, matching, as Brown comments, *Zeyher 4087. The lectotype.*

1231 Superficially like the previous, but the fruits have the characteristic beak indicating the specimen is *Moraea fugax* (de la Roche) Jacq. [= *M. edulis* (L.f.) Ker] (in spite of Brown's comment to the contrary).

3. *M. polyanthos* L.f.

1226 "α" A single poor specimen but clearly with the filaments entirely united; yellow anthers more than 5 mm long; style branches narrow and no style crests. It is the plant currently called *Homeria lilacina* L. Bol. (1920) and *M. polyanthos* is, of course, an earlier and valid name. *This is chosen as the lectotype*, as it has better preserved flowers of the two sheets bearing the name *M. polyanthos.*

1227 "β" Three specimens, of much branched plants with several leaves, the flowers poorly preserved; filaments are apparently united entirely, the anthers yellow, ca. 5 mm long; capsules 8 mm long. It is the same species as 1226, but with flowers in a poorer state of preservation.

The above determination of *Moraea polyanthos* was made after long, careful study, and I have noted above some important features of the specimens. Pertinent characters in making the determination are nature of the filaments, length of anthers, and style branch structure, specifically the presence or absence of prominent crests. The *Moraea* species "*M. polyanthos* sensu auct." has filaments free in the upper third, anthers ca. 5 mm long, and prominent style crests. *Moraea polyanthos* Thunb. (the type) and *Homeria lilacina* have united filaments, anthers 6 mm long, and narrow style branches without crests.

I am contradicting Brown's identification since the species lacking style crests is not a *Moraea* as currently understood, and its synonym *Homeria lilacina* had been known since 1920 (L. Bolus, 1920). Regrettably I am also contradicting myself (Goldblatt, 1976b) for earlier I had seen the Thunberg specimens and been satisfied with the identification of Thunberg's species with a common Cape *Moraea.* At that time I was unaware of the possibility of a good match with *H. lilacina*, which I know now to be identical to *M. polyanthos* sensu auct., non Thunb., in all except minute floral features.

The consequences of this change in interpretation of *Moraea polyanthos* are first, that the true *Moraea* species presently known as *M. polyanthos* must be called *M. bipartita* L. Bolus, the only available name for the plant. Second, the species currently *Homeria lilacina* L. Bol. becomes *Moraea polyanthos*, *H. lilacina* falling into synonymy here. I do not wish to transfer *M. polyanthos* to *Homeria*, since I am currently redefining this genus and plan to exclude *M. polyanthos* Thunb. (*H. lilacina*) from *Homeria*.

Thus *Moraea polyanthos* in my revisions of *Moraea* (Goldblatt, 1976a, 1976b) for both summer and winter rainfall areas of South Africa, becomes *M. bipartita*. Inclusion of *M. polyanthos* Thunb. (*H. lilacina*) in *Moraea* is the subject of a detailed paper (Goldblatt, 1980) on reevaluation of the generic limits of *Homeria*.

4. *Moraea crispa* Thunb.

1214 The collection consists of two plants which lack complete flowers today; plants each have a branched stem, and solitary, basal, channeled and twisted leaf. Leaves of both specimens are crisped along the margins. The species is most like the plant currently known as *Homeria rogersii* L. Bol. except that no collection of *H. rogersii*, a widespread Karoo species, has crisped leaves.

We should accept that as Thunberg placed *Moraea crispa* in *Moraea*, it lacked style crests, a feature he and Linnaeus fil. considered characteristic of *Iris*, and thus *M. crispa* conforms with present concepts of *Homeria*. *Moraea crispa* had a blue flower, and this strengthens the belief that it and *H. rogersii* are the same species. There thus seems very little doubt that *M. crispa* and *H. rogersii* are the same plant, and I therefore propose reducing *H. rogersii* to synonymy in *M. crispa*. I feel confident that further collecting will result in the discovery of a crisped-leafed form otherwise conforming to *H. rogersii*, which would then compel the name change made here. As I am currently redefining *Homeria* and *Moraea* (Goldblatt, 1980) I do not wish to propose a new combination here. *Moraea crispa* is probably most closely related to *M. polyanthos*, and may remain in *Moraea*.

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PALYNOLOGY AND SYSTEMATICS: THE TWENTY-FIFTH SYSTEMATICS SYMPOSIUM

RICHARD C. KEATING[1]

The study of pollen and its contribution to systematic and evolutionary studies was the theme of the Twenty-fifth Systematics Symposium. More than 300 systematic biologists attended the meeting held in the Garden's Lehmann Building, 20–21 October, 1978. The symposium was sponsored by a grant from the National Science Foundation.

As with many other biological disciplines, the study of pollen developed along with the optical microscope. In the decades prior to 1950, Scandanavian botanists, especially, developed stratigraphic palynology to a high science. It proved to be a powerful tool in studies of paleoecology and paleoclimatology. The growing reference collections of identified pollen preparations provided a basis for comparative studies which have remained a strong adjunct of plant systematic research to the present. Another discipline with its roots in the nineteenth century, plant-animal coevolution, has become quite visible in recent years. Pollination mechanisms are now recognized as having direct adaptive significance to the survival of both plant and animal species. That topic was discussed in the Twentieth Systematics Symposium in 1973 (Davidse, 1974).

This symposium was initiated by Jan Muller who described exine characters of angiosperm pollen in relation to their origin, structure and function. In the presentation by Joan Nowicke and John Skvarla, the order Centrospermae was used to demonstrate the potential influence of pollen morphology in higher order systematics. Robin Thorp described behavioral and structural adaptations of bees for collecting pollen. Donald Stone's discussion of *Heliconia* pollen and the pollen of some zingiberaceous relatives emphasized that the lack of an exine in those genera makes it necessary to handle such pollen by more careful methods than those traditionally used by palynologists. James and Audrey Walker's paper on pollen of the Myristicaceae showed the value of pollen in that ranalian family in defining generic limits and in confirming previously suggested trends of pollen

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evolution. Alwyn Gentry's and Spencer Tomb's paper on palynological evidence for redefinition of genera of Bignoniaceae provided a note of caution. Taxonomic confusion has resulted from using pollen evidence in isolation from other aspects of the biology of that family. The evening address by John Heslop-Harrison was given on pollen walls as adaptive systems. The pollen features discussed in relation to systematics during the day took on functional and adaptive significance in this presentation.

One of the striking trends of recent years has been the heavy use of the scanning electron microscope in most systematic palynological research. This tool, in addition to transmission electron microscopy, has supported important gains in our understanding of pollen characters and the trends of specialization regarding them. It is doubtful, however, that the newest tools will take over the field entirely. Stratigraphic palynologists and others who need to identify a variety of pollen types consolidated from sampling techniques will continue to depend on the light microscope.

Upon reflection, it seems clear to me that advancements in this field have not really been as tightly linked to technological developments in instrumentation as one might think at first. Nineteenth century botanists had quite adequate lenses available to them. A look at the pollen illustrations in Mohl (1834) and Fritsche (1837) will demonstrate an extraordinary rendering of detail. They presented extensive data on structure, sculpture, and apertures. Microscope objectives of short focal length and good resolution were available by 1827. By 1886, oil immersion lenses were manufactured which exceeded the numerical aperture of today's best commercially available objective lenses (Bradbury, 1967).

Notwithstanding the subtle distinctions which can be made using electron microscopy (Nowicke and Skvarla, this symposium), I submit that during the twentieth century, the growth of palynology as a discipline has been predominantly intellectual. Very few significant contributions have been dependent on the new instruments. Instead, we note steadily more thorough sampling, better quantitation, the posing of more refined questions, and better synthesis. The usefulness of palynology has become so obvious that it is now routinely incorporated into most systematic and evolutionary studies.

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FORM AND FUNCTION IN ANGIOSPERM POLLEN[1]

JAN MULLER[2]

ABSTRACT

In pollen morphology, as for other characters, the relation between origin, form, and function is basic for taxonomic interpretation. Physicochemical limitations to form development, structures inherited from gymnosperm ancestors, and newly evolved structures are reviewed from this point of view for a few selected angiosperm pollen types. The divergence of structures in closely related taxa suggests that pollen characters may evolve quite independently from other characters and are determined by a highly complex set of factors related to survival during transport and germination. For size and spinosity correlation with flower characters and pollination type is apparent in some cases. Special attention is given to harmomegathic functioning of the pollen grain as a whole, evidence for transfer of function is presented, and two new evolutionary trends are recognized. Peristasy involves reduction of colpate ectoapertures with retention of endoapertures, sphericity, and an exine structure distributing harmomegathic stresses equally over the surface. Latistasy results in a latitudinally oriented harmomegathic stress pattern and has been achieved in different ways. The independent origin of such trends in unrelated taxa is stressed.

In evaluating the significance of pollen characters, be it for taxonomic purposes or for interpretation of the fossil record, it is essential to consider the pollen grain as a functional unit. In the early days of pollen morphology, culminating in Wodehouse's classic *Pollen Grains*, which was published in 1935, exine morphology was generally studied in relation to intine development and behavior of the wall during changes in humidity of the environment and germination. With the introduction of acetolysis by Erdtman in 1934, attention became focussed more on the sporopollenin skeleton, revealed in intricate detail by removal of cytoplasm, intine, and outer fatty substances. The wealth of information which this method produced was first summarized in the monumental *Pollen Morphology and Plant Taxonomy* by Erdtman in 1952. While the introduction of scanning electron microscopy led to an even greater emphasis on the intricate details of exine architecture, transmission electron microscopy, especially when applied to ontogeny, provided a new impetus to the study of the entire grain. Moreover, a renewed interest in the physiology of the living grain (Heslop-Harrison, 1971a, 1971b, 1976) has stimulated an integrated study of all characters, which should ultimately lead to a pollen ecology.

When the present contribution, nevertheless, appears to concentrate mainly on the exine, this is because it incorporates a large number of taxonomically important characters which can be easily studied from herbarium specimens and also because, perforce, fossil pollen studies are entirely based on the exine skeleton. Its main purpose is to provide on this base a survey of certain widespread morphological phenomena, to consider their possible functional significance and thus to contribute to a better understanding both of their taxonomic significance and their value for interpreting the fossil record.

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EXINE STRATIFICATION

As is well known, the angiosperm pollen wall generally consists of a cellulosic intine and a sporopollenin containing exine. Although the proportion between these two basic layers may vary, it is only in certain hydrogamous plants such as *Zostera* that the exine is totally absent. This indicates a protective function for the exine against adverse atmospheric conditions.

The exine in its complete development consists of an inner endexine and an outer ectexine. Both layers can be distinguished by stain differentiation as first demonstrated with LM by Faegri (1956) and later confirmed with TEM by Larson et al. (1962). In some cases the endexine may be absent (Palmae, Thanikaimoni, 1970), while in others it frequently is thickened near the apertures.

The endexine generally has a more uniform structure than the ectexine but may show lamellations near the aperture or, as Van Campo (1978) has recently emphasized, interior sculpture. Its ultrastructure is basically lamellated, but this may be masked by sporopollenin deposition later (Heslop-Harrison, 1971b: 88).

The ectexine shows more variation in structure, ranging from virtually homogeneous in *Degeneria* (Dahl & Rowley, 1965), granular as in *Piptostigma* (Van Campo & Lugardon, 1973), or columellate with or without an inner sole and outer tectum as in many angiosperms. The sole (formerly called foot-layer, cf. Cerceau-Larrival et al., 1975) may be homogeneous or laminated, while the tectum may bear various types of sculptural elements such as warts or spines. Frequently columellae and tectal elements combine to form complicated structures.

Two main questions arise regarding this radial differentiation in the exine:

1. What is the phylogeny of the different layers?
2. What is their function?

Before we can attempt to answer these questions a short review of exine ontogeny is necessary. In the case of the columellar exine, sporopollenin accumulates on lamellae of unit-membrane dimensions within the primexine, and, very early in the ontogeny, radially oriented probacula develop, which subsequently expand at their tops to form the tectum and at their bases to form a sole. The endexine develops later (Heslop-Harrison, 1971b).

In the case of the granular exine, it is not yet clear whether a different system operates, but the fact that transitional structures are known, such as described in Annonaceae by Le Thomas & Lugardon (1976), suggests that the difference may not be fundamental and that columellae may in fact be composed of linearly fused granules, the linear orientation being supplied by radially oriented lamellae.

However, the situation in *Polyceratocarpus* (Annonaceae) described by Le Thomas & Lugardon (1976) in which the exine essentially consists of a granular mass with a loose accumulation of larger granules on the inner side, becoming more fine grained and compacted outward, suggests a system of indeterminate growth by apposition of material from the inside. This is, of course, very different from the precisely controlled development of a typically columellar exine.

Doyle et al. (1975) have shown that granular exines occur both in gymnosperms and angiosperms, but that columellar exines are at present only known from angiosperms, although Klaus (1977) has recently described columellar structure below the alveolar zone of the ectexine in *Pinus*. However, the extinct

gymnospermous pollen type *Classopollis* has a structure which is very similar to a columellar one (Pettit & Chaloner, 1964), and recently Cornet has discovered Triassic pollen grains of as yet uncertain affinities with a very distinct reticulate-columellate exine structure (Cornet, 1977; Doyle, 1978). This suggests that a columellar organization of sporopollenin may have evolved independently in different plant groups and may not be an exclusive character of the angiosperms.

The alveolar exine type characterizing many gymnosperms is not known from recent angiosperms, although transitions may have existed in the past between the radially oriented structural elements of the middle exine layer of cycads or saccate conifers and the columellae layer of angiosperms. This possibility is suggested by the occurrence of *Clavatipollenites*-like grains in the middle Jurassic of Sweden (Tralau, 1968).

The endexine, as first pointed out by Doyle et al. (1975), is more uniformly present and laminated in gymnosperms than in angiosperms, and these authors propose an hypothesis involving reduction and subsequent reelaboration of the endexine during the transition between the two groups. As pointed out before, the basic structure of the young endexine in angiosperms is lamellate, and this would be evidence for homology, although certainly the elaboration of endexine characters, especially near the endoapertures, in this group is unmatched in gymnosperms.

A new element in angiosperm exines is the sole, which does not appear to be present in any gymnosperm pollen grain. Interestingly, this layer is either homogeneous or laminated as in certain Annonaceae (e.g., *Isolona*: "couche basale feuilletée lamellaire," Le Thomas & Lugardon, 1976) and Dipterocarpaceae (e.g., *Vatica*; laminated basal layer, Maury et al., 1975). It may be noted that in both cases this laminated layer belongs to the ectexine and is equivalent to the sole, and, moreover, that it represents, no doubt, a derived condition. Again, this demonstrates how comparatively easily in unrelated plant groups the basic process of sporepollenin deposition can be modified in any layer of the exine.

Undoubtedly such changes occur in response to selective pressure, and this brings us to the question of functional significance. Basically, any exine structure is a compromise between the protective, the harmomegathic, and the reservoir function. The protective function is evident in closed, sealing layers such as a homogeneous sole or a closed tectum. The harmomegathic function, which is the ability to absorb bending stresses such as occur during desiccation, as Wodehouse (1935) was the first to point out convincingly, has resulted in structures which prevent rupture of the exine. The reservoir function may be connected with characteristic cavities which are so widespread in the pollen of many angiosperm families, and which hold tapetum-derived materials (tryphine) that play a significant role in producing an adhesive surface ("pollenkitt") or as recognition substances. In fact, Heslop-Harrison (1976) considers the columellate layer to be the culmination of an adaptive trend for favoring outbreeding by conveyance of sporophytic recognition substances.

Since the cavities found in many gymnosperm pollen grains do not appear to carry such substances (Heslop-Harrison, 1976), it may be that their origin is related to structural strength. The tubular-alveolar structure in cycads enforces a certain rigidity, at least in the extraapertural regions, while the columellar an-

giosperm exine is probably relatively more flexible, especially the open reticulate-columellar structure. It is also of interest that the laminated endexine of gymnosperms appears more flexible than the ectexine. In this view the columellate-tectate angiosperm exine may represent also a culmination of a trend towards a more equalized distribution of bending stresses over its entire thickness. As discussed by Muller (1969) and Bolick (1978), the radially oriented columellae would serve as elements absorbing compressive forces, while the tectum would form a tensile element. The function of the endexine has at the same time become more closely related to the apertures.

Of interest in this context is the granular exine. Structurally it behaves quite differently to bending stresses, and it does not appear to have a well-developed reservoir function. Also, its potential for combining with tectate structures into the complex exine architecture such as occur in many highly evolved angiosperm pollen types, as for example in Compositae, appears limited.

This may explain the prevalence of granular type exines in many wind pollinated "amentiferous" taxa such as *Juglans* (Van Campo & Lugardon, 1973), *Ulmus*, *Alnus* and *Betula* (Nilsson et al., 1977). Here the granular infratectal structure is correlated with a rather uniformly thin exine, a lack of tryphine causing a dry surface, and an absence of any sculptural development of the tectum except small spinules. Again, it is obvious that a similar structure has evolved in close response to similar ecological requirements, i.e., wind pollination in not closely related taxa, probably in late Cretaceous time during evolution from the Normapolles complex (cf. Doyle, 1978).

In contrast to this is the situation in *Vigna* and *Phaseolus*, recently described by Stainier & Horvat (1978). These two leguminous genera which have a very similar flower morphology and presumably also pollination, differ in their exine structure. In *Vigna* a granular infratectal structure is present, and correlated with simple porate apertures, while *Phaseolus* pollen is characterized by a columellar structure and complex colporate apertures. This difference is here closely correlated with taxonomy, although its functional significance is obscure.

APERTURES

The local modifications of the exine structure generally termed apertures have early drawn the attention of pollen morphologists, and by now it is clear that in angiosperms a large range, from simple to complex apertures, often integrated with intinal differentiation occurs. Functionally, apertures act as regulatory harmomegathic structures, as contact points for the exchange of intine-bound recognition substances and, finally, as exits for the pollen tube (Heslop-Harrison, 1976).

Wodehouse (1935) was the first to point out that the earliest angiosperms had inherited the distal fold or sulcus from their gymnosperm ancestors, and that a large part of the morphologic variability of angiosperm apertures is related to the elimination of the distal aperture and its replacement by equatorial or peri-dispersed apertures. It appears probable that this change was related to selection for increased efficiency in pollen-stigma interaction, but it obviously also involved a complete reconstruction of the harmomegathic stress system. A first problem

to be discussed is whether the distal sulcus is strictly homologous with equatorially oriented, folded ectoapertures or colpi.

In general, spindle orientation, cleavage pattern, and polarization in the early tetrad stage appear to determine aperture location (Huynh, 1976). In the case of distal apertures, polarization is the dominant influence, as shown by Heslop-Harrison (1971a) for *Lilium,* where undivided mother cells do not develop an aperture. In Gramineae Christensen & Horner (1974) have demonstrated that influences outside the mother cells determine the location of the single aperture which is therefore not distal in the strict sense (Faegri, 1978; Huynh, 1975).

For the equatorially tricolpate pollen type it has long been recognized that apertures are initiated at specific points in the developing tetrad in such a way that they are arranged in a paired position according to Fischer's law. Here the location of the apertures is thus determined not only by polarization but also by intracellular equal spacing and intercellular positioning, resulting in a paired arrangement. The equal spacing has been shown by Tammes (1930) to represent a least surface configuration. The paired position results according to Wodehouse (1935) from phragmoplast connections for which he presents a convincing picture of an abnormally developed *Cichorium* tetrad. However, recent ultrastructural studies have failed to show evidence for the existence of such connections due to very early development of a callose wall separating the tetrad cells. Moreover, it was already pointed out by Wodehouse (1935) that, in the abnormal case of a square *Cichorium* tetrad, two apertures formed by pit connections, while opposite these two, more apertures developed at points of the cell surface not in contact with the other surfaces.

It is also instructive in this connection to observe tetrads of stephanocolpate pollen grains such as occur in *Utricularia punctata* (Thanikaimoni, 1966). Here all colpi are positioned in equally spaced paired positions. This suggests strongly that aperture induction is coordinated for the tetrad as a whole before callose deposition on the phragmoplasts takes place, and that number of apertures and their equatorial location is genetically determined, while their equal spacing is the result of physicochemical forces acting over the entire surface of the sporocyte and resulting in a least surface configuration.

At the ultrastructural level, microtubules appear to be involved in this process, and the first visible indication of future aperture sites is a plate of endoplasmic reticulum attached to the plasmalemma. Rowley (1976) considers the process of aperture formation as essentially similar in such divers taxa as *Silene* (Caryophyllaceae), *Beta* (Chenopodiaceae), *Saintpaulia* (Gesneriaceae), *Parkinsonia* (Leguminosae), *Helleborus* (Ranunculaceae), *Citrus* (Rutaceae), and *Capsicum* (Solanaceae), while in *Epilobium* (Onagraceae) and *Tradescantia* (Commelinaceae) different processes appear to be involved. Also, Dickison (1976) stresses the fact that taxa may differ in this respect.

The change from equatorially arranged apertures to peri-dispersed ones, either colpate or porate, reflects loss of polarization and a take-over of aperture induction by forces leading to least surface configuration entirely. An interesting transitional case is the spiralization of apertures described for *Sidalcea* by Van Campo (1976) and in abnormally developed gigas pollen for *Utricularia* by Casper & Manitz (1975).

It is probable, though not yet proven by observation, that in the peri-dispersed arrangement positioning of apertures takes place for each microspore independently of its sisters in the tetrad. In this connection Waterkeyn & Bienfait's (1970) observations on *Ipomoea* pollen are of interest. These authors showed that here the callosic wall shows a thickness pattern directly related to the apertural configuration and assume that this callose template is primary. Earlier, Waterkeyn (1964) had already suggested that callose thickness differences reflect the orientation of the microspores in the tetrads and thus determine the distal pole and the position of the aperture. Willemse (1971) has described a similar phenomenon in *Pinus*, where callose formation is blocked at places where vesicles derived from the endoplasmic reticulum extrude, producing a template for the coming exine pattern. Also, Ford (1971) established for *Styphelia* that ectexine patterning is bound to the presence of callose. The hypothesis that callose functions in some way as a passive intermediate stage, transferring the transient cytoplasmic pattern as a stable template for subsequent primexine replication, therefore, seems an attractive one.

In this view, the peri-dispersed aperture configuration could result from no more than a slight difference in timing of the relevant processes, in such a way that initiation of apertures is delayed to a stage when the callose walls separating the young microspores have effectively severed polar gradients which were present before in the tetrad as a whole. As a consequence, the young microspores will tend to remain spherical, and forces leading to a least surface configuration of apertures will take over and cause a peri-dispersed distribution. It is clear that genetically this may be caused by minor mutations, and that this may easily happen in an identical way in quite unrelated taxa, which is, in fact, what is found in any survey of the taxonomic distribution of this character. This hypothesis could also form the basis for the successiform series first recognized by Van Campo (1967).

In this connection it may be pointed out that, according to Schwanitz (1953), polyploids which are often characterized by larger pollen grains with peri-dispersed apertures, have a lowered metabolism. This may have contributed to the postulated slight shift in timing of the various stages involved in the critical early phase of exine ontogeny. It may be added that extraapertural exine structure is rarely, if ever, affected.

The positioning of a large number of peri-dispersed pores, as in *Ipomoea*, differs in some respects from the configurations of peri-dispersed colpi. Tammes (1930) first showed that in the latter case the configurations found correspond to regular endospherical polyhedra. Wodehouse (1935) further elaborated on this and supposed that isotasithynic (= equilateral) stresses could produce a trischistoclasic pattern and that heterotasithynic (=unequal) stresses would lead to tetracolpate or loxocolpate configurations. His suggestion (Wodehouse, 1935: 185) that furrow configurations are the result of mechanical stresses now appears unlikely in view of the very early initiation of apertures, at a stage when the young microspores are still enclosed within the confines of the insulating callose wall of the meiocyte. Instead, the mathematical derivation by Tammes (1930) of the regular peri-dispersed aperture configurations from the point systems on a sphere appears sufficient explanation, provided colpi are equivalent to pores. He

has shown that for any given ratio between p, the radius of the touching circles, R, the radius of the sphere and the actual number of apertures preferred arrangements result, which for the lower numbers correspond to one of the five possible endospherical polyhedra. A further elaboration of this theory has been given by Fejes To'th (1964:226–237). In this view, which is close to that adopted by Van Campo (1976), the only "force" needed is the one causing equal spacing of initiation sites.

An extreme example of the operation of this principle is found in Malpighiaceae, where Lobreau (1967) could describe the various apertural configurations in strict crystallographic terminology. These variations appear here to be correlated with intergeneric differences.

Van Campo (1976) discussed the taxonomic distribution of her successiform series and showed that both taxonomic correlation (Centrospermae!) and independent origin in unrelated taxa is found.

The preceding discussion mainly referred to what may be termed primary apertures present in the ectexine, or ectoapertures. However, the endexine may develop secondarily endoapertures, either in combination or separately from the ectoapertures, indicating independent initiation, probably again made possible by a slight difference in ontogenetic timing.

In the normal case of a tricolporate grain, the endoapertures occupy the central equatorial position of each ectoaperture, but already in the heterocolpate grains the number of endoapertures is half that of the ectoapertures, although their position has not changed. In *Pardoglossum tubiflorum* (Boraginaceae) compound pores alternate with simple colpi (Clarke et al., 1979). The pores consist of a distinct circular endoaperture, covered with a finely verrucate membrane which can be interpreted as a reduced ectoaperture. The ectocolpi are of the normal narrow, invaginating type. It would be interesting to study the behavior of this pollen type during changes in humidity and while germinating.

A most intriguing case of displacement has been described by Clarke (1977) for *Lappula squarrosa* (Boraginaceae) where the plane in which the endoapertures are situated is oblique to the equatorial plane. Similar phenomena are known from Malpighiaceae and, as an abnormality, in *Lepisanthes* (Sapindaceae).

This emphasizes the different character of both types of apertures. While the ectoaperture is basically elongate (colpate) and only secondarily porate, the endoaperture located in the endexine is basically isodiametric and only secondarily elongate. The tricolporate aperture, which is phylogenetically younger than the tricolpate one, may thus represent the juxtaposition of an "inherited" colpus and a newly developed pore structure, and a large part of the diversity in higher dicotyledonous pollen types may reflect attempts to reconcile these phylogenetically, as well as functionally, different elements structurally. In a study of the pollen of *Plagiopteron* (Plagiopteraceae) Baas et al. (1979) have discussed this problem.

It is significant in this connection that the earliest tricolpate pollen types from the lower Cretaceous show no trace of endoapertures. The earliest manifestation is a slight bridging or constriction of the colpus membrane, the "geniculus" of Potonié (cf. Stanley & Kremp, 1959). This development has the important structural consequence that the infolding of each colpus is restricted to two areas

poleward of the equatorial constriction of each furrow, effectively diminishing the total volume accommodation possible. In a later stage the endoapertures become more clearly outlined in the endexine, which is soon followed by a situation in which endexinal thickenings or costae surround the endoaperture. These costae may be annular, present on the polar sides only, or restricted to the corners between equatorially elongated endoapertures and the superposed colpate ectoapertures. Also, the colpi themselves may develop costate thickenings along their margins. In general these appear to represent different solutions to the problem of combination of a fixed point structure within a folding structure. In the more extreme cases, the pore is converted into a protruding structure, taking over part of the harmomegathic functioning of the colpi which may finally disappear altogether. In other cases the endoapertures become equatorially extended and, ultimately, fused to form a ringlike structure which is frequently bordered on the polar sides by endexinal costae. This case, which will be discussed more in detail later, occurs in certain pollen types found in Lentibulariaceae, Polygalaceae, and Rhizophoraceae. Here the harmomegathic functioning is transferred from the colpi (meridional folding structures) to the endoapertures (equatorial folding structure). Other specializations are the H-shaped structures in Cornaceae, described by Ferguson (1977) and the endoapertural folds or "replis" of Celastraceae studied by Lobreau-Callen & Lugardon (1973).

It is clear that many of these developments are of considerable taxonomic significance since they seem to be restricted to a part of the higher dicotyledons. In Caryophyllales and Papaverales endoapertures are very rarely developed. In Ranunculaceae also they appear to be absent, but in other families assigned to Ranunculales they may be more frequent (e.g., Lardizabalaceae, Menispermaceae). In Trochodendrales they are weakly developed as in Platanaceae (Hamamelidales) and Eucommiaceae (Eucommiales). In Fagales the genus *Quercus* still represents all transitions between colpate-colporoidate-colporate, while *Fagus* has truly tricolporate pollen. Didymelaceae are remarkable in having two well-developed endoapertures per colpus and resemble in this respect the Albian genus *Hexaporotricolpites*.

In contrast, the subclasses Dilleniidae, Rosidae (with the exception of the order Proteales), and Asteridae have basically colporate apertures, although secondary modifications may have caused loss of endoapertures (Dipterocarpoideae) or loss of colpate ectoapertures, either leading to "pororate" types, in which the ectoapertures have become porate, or to cryptoporate types, in which any trace of ectoapertures has been eliminated and a uniform sculpture covers the endoapertures. This last phenomenon will be discussed more in detail later.

EXINE ARCHITECTURE

In this chapter those features of the extra-apertural exine which form what is commonly called structure and sculpture will be discussed. Since these two terms are often hard to separate, especially in the more complexly built exines, Walker & Doyle's (1975) suggestion to use the term architecture is followed here. Structure will be used as a term denoting a specific type of architectural element. Basically three different structural types can be distinguished:

A. Columella-derived structures, mostly with a reticulate architecture.
B. Tectal structures, mostly spinose or verrucose supratectal structures.
C. Combined structures such as are found in the spinose exines of Compositae.

The fossil record indicates that an evolutionary progression A → B → C has taken place. The factors determining this have no doubt been very diverse. Transport, reservoir, and protective requirements must have been intricately interwoven, while the structures found in large grains must also have been adapted to growth during development. This makes it necessary again to start with a discussion of ontogeny. For group A it is clear that the structures are close to the original probacula pattern which is determined very early in the ontogeny in the primexine. For *Zea*, Skvarla & Larson (1966) have shown that the precise location of the probacula is induced by microtubules. The tops of the probacula often fuse more or less completely rather soon, and the resulting tectum may have a more or less open structure depending on the balance between sporopollenin deposition and rate of expansion of the exine.

Although originally probacula initiation may have resulted from a basic least surface configuration of the microtubules, in many cases further control of patterning is related to the apertures. Also, the bacula pattern itself may become reticulate or linear, forming single or multiple rows. The way in which these more specialized arrangements originate is as yet unknown.

The larger structures which develop from the tectal surface appear to be determined mainly by the underlying columellate patterns but may also follow independent least surface configurations when developing during the later phase when tapetal deposition of sporopollenin takes place, as shown for *Tagetes patula* by Heslop-Harrison (1969). This independence is especially clear in the case of some of the micro-patterns revealed by SEM. While in the case of Gramineae pollen, the pattern of supratectal spinules rather closely conforms to the underlying columellae pattern, in the case of *Plantago* their pattern is independent and closely follows a least surface configuration. In Fig. 1 this pattern is shown to develop independently of the underlying operculate aperture, as if deposited on a thin outer covering membrane. For *Myriophyllum* Aiken (1978) has shown that such a pattern indeed develops relatively late in the ontogeny. In other case the outer surface is covered with a much more dense structure. Some of these micropatterns, like those in *Quercus coccifera* (Fig. 2), show a remarkable resemblance to patterns of coral growth such as found in the genus *Goniopora*. This is no doubt due to the fact that both processes take place in a liquid environment saturated with the dissolved building material, respectively sporopollenin and calcium carbonate, while the growth pattern of the sporopollenin receptor surfaces must be similar to that of the coral organisms, albeit on a vastly different scale. It is likely that differences in micropatterns which, as Smit (1973) has shown, characterize different groups of oaks are due to different branching patterns of the receptor molecules.

The combined structures represent a close integration of both types of processes. The best examples of this group are found in the echinate structures which have developed in such variety in many unrelated angiosperm groups.

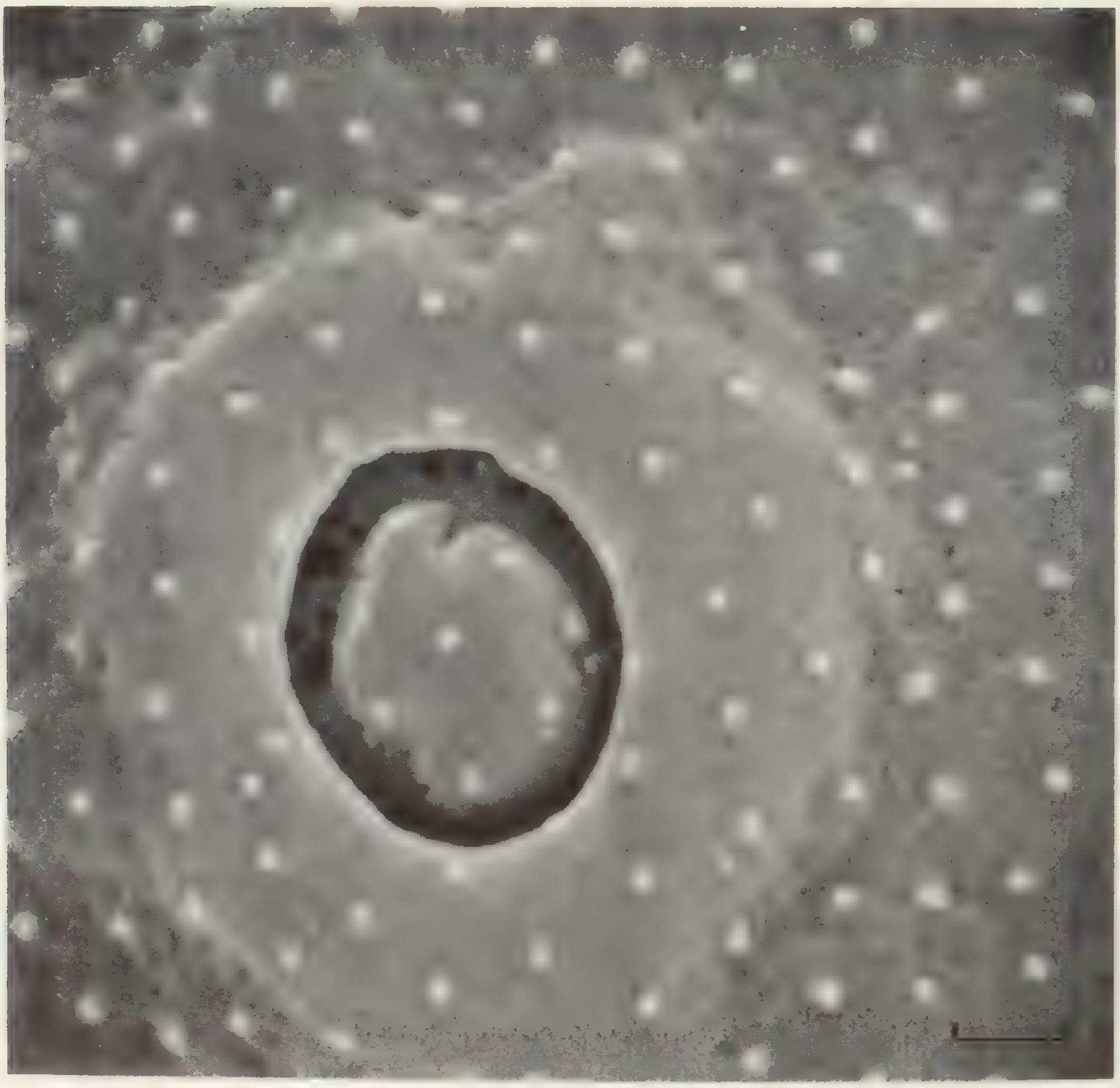


FIGURE 1. *Plantago lanceolata* (Plantaginaceae). Surface view of a pore showing operculum, invaginated and locally perforated pore membrane, and protruding annulus surrounding the pore. The outer surface of the tectum appears irregularly wavy with very fine scattered perforations, while the surface of annulus and operculum is more dense and smooth. The white dots represent a regularly spaced pattern of minute verrucae. This hexagonal pattern is independent of the underlying aperture structure. SEM, acetolyzed, 10,000×. Courtesy Dr. C. G. S. Clarke.

In Fig. 3 some examples are given which demonstrate how various exine layers are involved. Recently Rowley & Dahl (1977) have shown in great detail the ontogeny of spine structure in *Artemisia* (Compositae). It will be clear that for such a complex chain of events to evolve, a long history starting with the simple probacula-derived pattern of early angiosperm pollen types must be postulated, and it is therefore not surprising that Compositae pollen is one of the latest pollen types to appear in the fossil record (Oligocene, cf. Muller, 1970).

Another example of an integrated structure is the exine of *Dipterocarpus*. Here tectum and columellae have been transformed into urn-shaped structures, fused into a structure of higher order with concomitant disappearance of the endexine, while the sole has been reduced from a thick solid layer to a thin laminated one (Maury et al., 1975). The ontogeny of this structure has been traced to the earliest phase of sporopollenin deposition and, as shown in Fig. 4, is already largely developed. The subsequent expansion to the mature pollen grain, shown graphically in Fig. 5, involves a 3-fold increase in size and shows how the basic

FIGURE 2. *Quercus coccifera* (Fagaceae). Surface view of extraapertural exine. The tectum is densely covered by irregular agglomerations of elongated rugulate elements. This very fine structure appears accretionary in nature and probably was deposited independent of underlying columellate patterns. SEM, acetolyzed, 20,000×.

exine architecture is retained. The growth curve for *Dipterocarpus* pollen indicates a visco-elastic growth pattern and, exceptionally, SEM has revealed ringlike patterns, visible in Fig. 4E, which may reflect this mode of growth which is, of course, markedly different from the accretionary surface pattern referred to earlier. Many other complex exines must also be adapted to such a retention of shape during rapid growth and sporopollenin accretion. For a more detailed discussion of the processes involved, reference must be made to Heslop-Harrison (1971b: 85–86).

A functional analysis of the exine architecture of mature angiosperm pollen involves a study of the following aspects:

A. The protective function, mainly against adverse atmospheric conditions such as dryness and UV radiation. The original way in which the exine protects the living content may have been by a solid sheet such as is common in ferns and also in *Degeneria* and other primitive dicotyledons. In the open structures developed later, the protective function of the sporopollenin may have been partly transferred to what Heslop-Harrison (this symposium) has termed the lipid seal. In open reticulate structures the lipid layer would be retained by capillary forces.

B. The harmomegathic function in the sense of Wodehouse (1935), accommodating the unavoidable changes in volume caused by fluctuations in relative humidity of the atmosphere. Special attention must be drawn here to the traumatic moment occurring during anthesis at the desiccation phase of the anthers, when the pollen grains suddenly are transferred from a liquid to an atmospheric environment. It appears likely that this is the moment of maximum stress for the

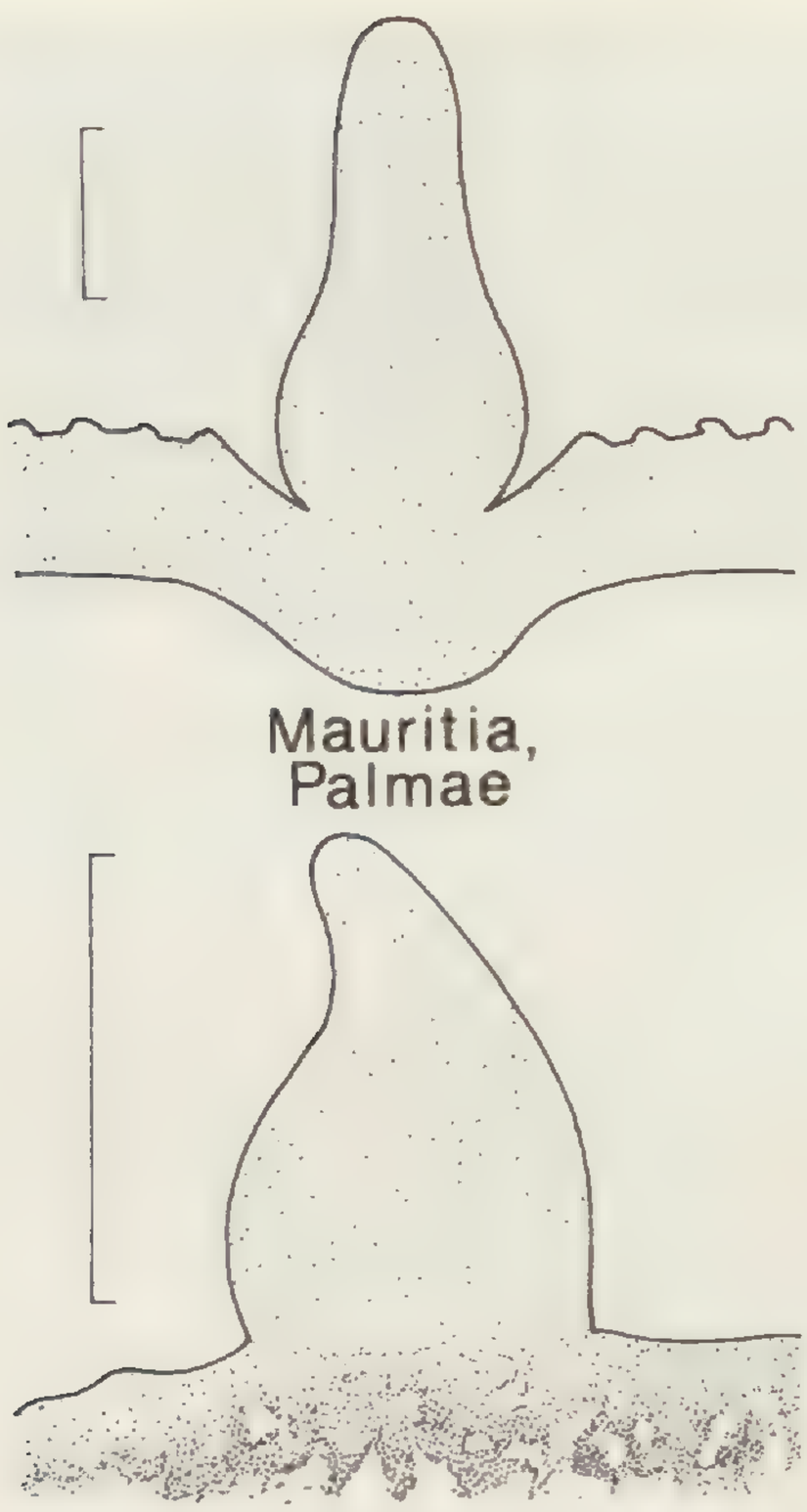


FIGURE 3. Spine structure in angiosperm pollen. Scale: 1 μm.

exine. It has to be strong and flexible enough to prevent collapse at this critical phase of drying out. Payne (1972) has shown the forces involved to be considerable and has argued that a large part of exine architecture has evolved in response to these factors, rightly emphasizing, however, that the pollen grain functions as a whole, apertural and extra apertural structures being closely integrated. McGlove (1978) has recently argued that the tetrad of *Epacris* functions as a single harmomegathic unit.

C. The reservoir function, stressed by Heslop-Harrison (1976), who has shown that the exine cavities are filled with many other physiologically active substances besides lipids. The storage of recognition substances here would explain the frequency of exines with an open architecture, adapted to rapid contact with the stigma, ensuring that recognition is not entirely dependent on an aperture touching the stigma surface.

Hesse (1978) has recently studied in detail these lipids which he considers to be mainly functioning as sticky "pollenkitt." Of interest is that in some pollen types with a closed tectum (*Aquilegia, Castanea, Quercus*) the intracolumellar cavities are entirely filled with lipids, while the outer surface is hardly sticky. It would appear likely that in such cases the sealing function is more significant.

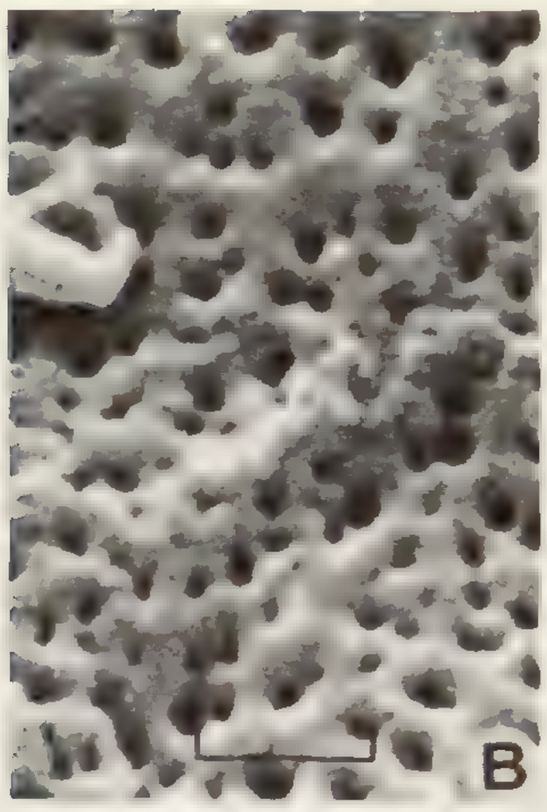
D. The clustering function, related to mode of dispersal. This aspect has early caught the attention of pollen morphologists and led to the well-known distinction of smooth-surfaced, dry pollen of wind-pollinated taxa and oily, often spinose or reticulate pollen of insect-pollinated taxa.

The significance of oily surface layers was already studied in detail by Knoll (1930) and Pohl (1929, 1937) and, as mentioned above, recently by Hesse (1978). However, it must be pointed out that certain insect-pollinated flowers have small, smooth dry pollen which is adapted to the special way in which the pollen is shaken out of the anthers through a small opening. This was already described by Troll (1928) for *Galanthus* and occurs in many other families as well. Beattie (1971) has studied the mechanism in *Viola,* while, according to Macior (1968), visiting insects often gather pollen by wing vibration from similar anther types in *Pedicularis* (Scrophulariaceae) and *Dodecatheon* (Primulaceae).

Shape

Distally monosulcate angiosperm pollen grains, such as those of *Magnolia,* have generally retained the typical elongated boatshape found, for example, in *Cycas* and other gymnosperms. However, rather early in the fossil record and especially in the *Clavatipollenites* lineage, a tendency towards a more spherical shape becomes manifest. With the origin of the tricolpate type, formed in a tetrahedral tetrad, a basically spherical shape develops which can subsequently be modified by differential growth in an equatorial, polar, or interapertural direction leading to oblate, prolate, or trilobate shapes, respectively. These shape modifications are often closely integrated with apertural and structural modifications.

It is considered likely that the change in shape was primary and that the change from a single slitlike sulcus to the tricolpate condition was secondary. This is suggested by the circumstance that a single inwardly folding sulcus on a boat-shaped grain forms a well-integrated harmomegathic system, while the same aperture on a sphere creates unequal harmomegathic stresses which can only be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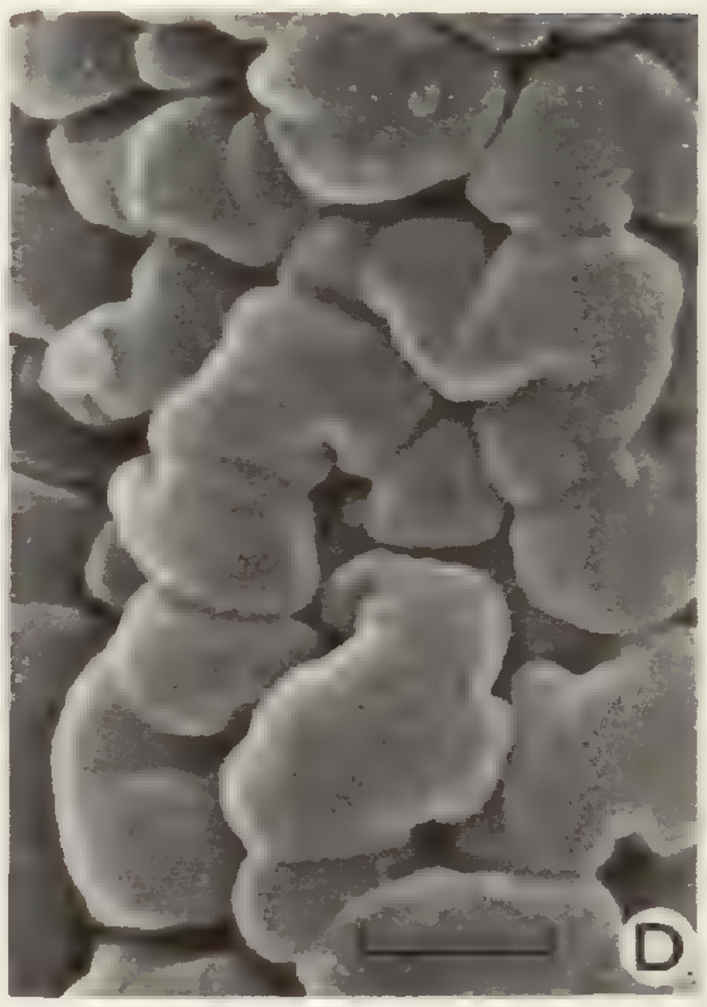
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equalized by shortening of the slit with, as logical end-product, a single round pore. However, this entails a reduction of the germinative area and the development of the tricolpate type may be seen as the achievement of both a more efficient harmomegathic stress pattern with a better relation between volume reduction and stress distribution and an increase in germinative area, promoting fast and efficient stigmatic contact.

A major part of the subsequent evolution of the tricolpate type consists of further specialization towards controlled harmomegathy and the shape modifications can be related to this. In the first place the relative increase of growth of the polar axis, the trend towards longiaxy, can be seen as a recreation of the elongated shape, to which, as pointed out earlier, the colpate aperture is best adapted. Compared to the boat-shaped sulcate type, the orientation of the long axis is changed from equatorial towards polar.

The opposite trend towards relative shortening of the polar axis, the trend towards breviaxy (Van Campo, 1966), is also widespread and, as mentioned before, generally associated with a striking modification of the apertural system. In extreme cases this leads to the reduction of the ectocolpi and the development of porate apertures. The shape is often further modified in a triangular one with pores at the angles or interangular. In such pollen types the disappearance of the colpi means a transfer of the harmomegathic function from the colpi to different exine structures, examples of which will be discussed later on.

Size

Wodehouse (1935) has shown in an excellent way how transport conditions often limit the size of angiosperm pollen grains. The majority fall in the 20–40 μm range and are adapted to easy liberation from the anthers, moderate wind transport, and optimal adherence both to insect vectors and to the stigma. The typically wind-pollinated grains also fall in this range. Exceptions are the large pollen grains, mostly transported by animal pollinators, and the very small ones which are often associated with highly specialized pollination systems. In rare cases such as the paper mulberry, vividly described by Wodehouse (1935), an explosive device liberates the extremely small pollen grains. Gehrmann (1911)

←

FIGURE 4. Exine growth in *Dipterocarpus* (Dipterocarpaceae).—A–C: *D. gracilis*.—D–E, G: *D. nudus*.—F: *D. confertus*.—A. Early stage showing partly doubled-up exine with urn-shaped invaginations (arrows) without any distinction between columellae and tectum. The laminated basal layer or sole(s) is still very thin and loosely attached to the invaginations. TEM, glutaraldehyde-OsO_4 fixation, stained with uranyl acetate and Reynold's lead citrate, 20,000×.—B. Very early stage. Exine surface rather flat with a granular structure and scattered perforations. At top left, urn-shaped Ubisch body. SEM, acetolyzed, 10,000×.—C. Early stage, probably corresponding to A. The exine surface starts developing the convoluted ridge system. At top left, another Ubisch body. SEM, acetolyzed, 10,000×.—D. Middle stage, with strongly convoluted and compressed exine ridges hiding the urn-shaped depressions and with an indistinctly finely striated surface. SEM, acetolyzed, 10,000×.—E. Mature stage, showing fully expanded exine, exposing the depressions and occasional bridging lower ridges. Surface of exine clearly finely striated probably resulting from sporopollenin accretion on an irregularly stretching exine. SEM, acetolyzed, 10,000×.—F. Sectioned exine showing the urn-shaped invaginations to the bases of which the thin basal layer is attached. SEM, acetolyzed, 4,200×.—G. Mature grain showing the uniform exine pattern and the narrow colpus which will only invaginate slightly. SEM, acetolyzed, 1,000×.

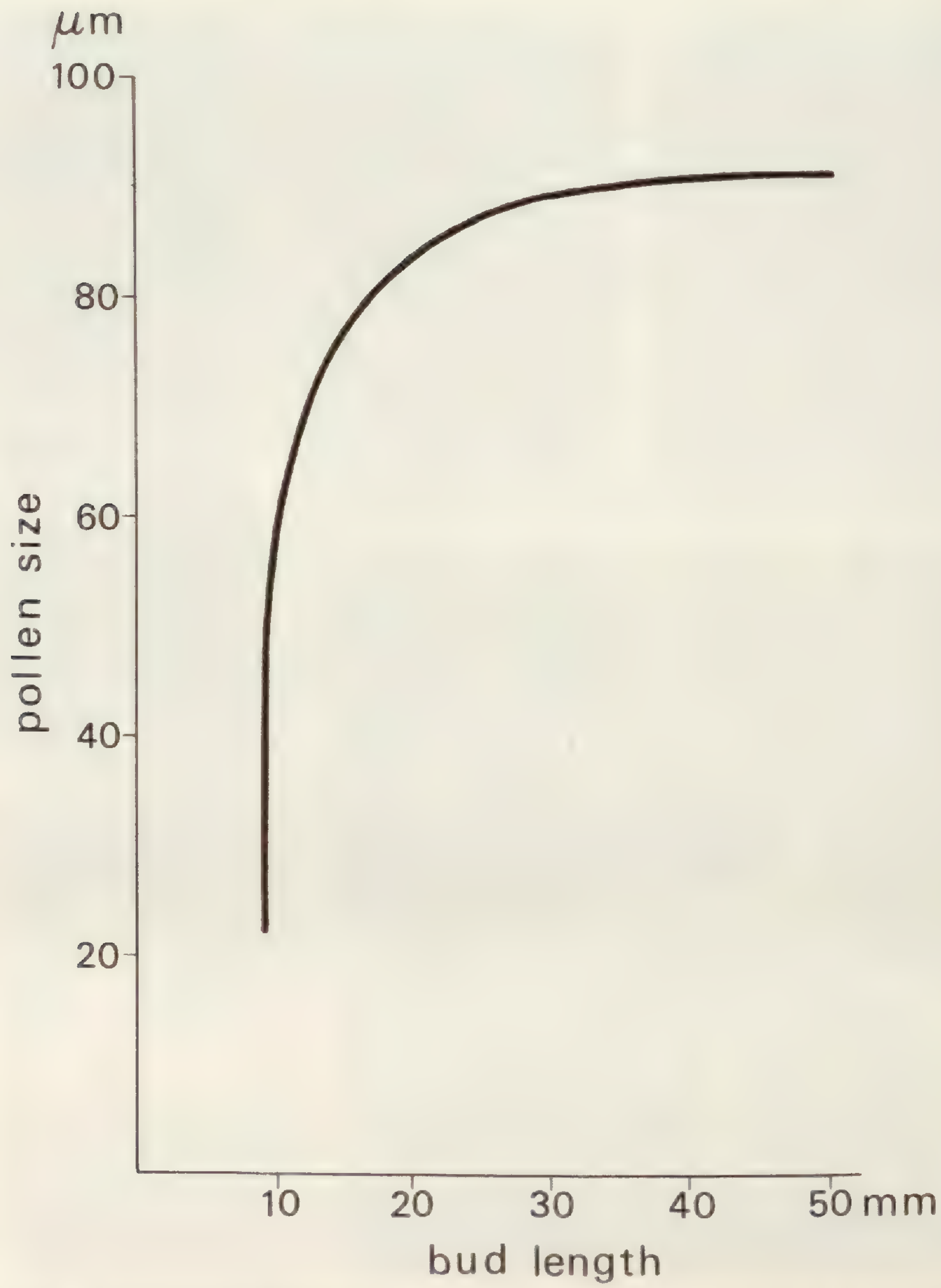

FIGURE 5. *Dipterocarpus caudiferus* (Dipterocarpaceae). Growth curve of acetolysis resistant exine.

had already described a similar mechanism for *Bruguiera* (Rhizophoraceae; cf. also Tomlinson, 1977).

Whitehead (1969) has discussed in more detail the significance of pollen size for wind-pollinated plants by considering aerodynamic principles. He emphasized that very small grains (<20 μm), although dispersed widely, cannot be captured efficiently by the stigma, unless it is thinly branched like in grasses.

Wodehouse (1935) also pointed out that primary evolutionary changes in size may have profound influences on exine morphology: the smaller the pollen grain, the less complex architecture and aperture structure.

In this connection attention must be drawn to the relatively small size of many

TABLE 1. Relation of chromosome number with pollen size.

+ Correlation				No Correlation		
A, Intraspecific		B, Interspecific	C, Intergeneric	A, Intraspecific	B, Interspecific	C, Intergeneric
Campanulaceae, *Campanula patula*, 1; *C. rotundifolia*, 1; *Lobelia syphilitica*, 2.	Labiatae, *Monarda fistulosa*, 2; *Salvia pratensis*, 2; *S. splendens*, 2.	Campanulaceae, *Campanula*, 1.			Dipterocarpaceae, *Shorea*, 14; *Hopea*, 14.	Acanthaceae, 18.
Compositae, *Cichorium intybus*, 3; *Thelesperma* sp., 4; *Tridax coronipfolia*, 4.	Leguminosae, *Trifolium hybridum*, 2; *T. incarnatum*, 2; *T. pratense*, 2; *T. repens*, 2.	Compositae, *Thelesperma*, 4.			Onagraceae, *Gayophytum*, 15.	Cactaceae, 19.
Cruciferae, *Arabidopsis thaliana*, 5; *Brassica oleracea*, 3; *B. rapa*, 3; *Raphanus sativus*, 3; *Sinapis alba*, 3.	Polygonaceae, *Rumex patientia*, 3.	Gramineae, *Aira*, 21; *Andropogon*, 11; *Avenella*, 21; *Deschampsia*, 21.			Solanaceae, *Nicotiana*, 16.	Dipterocarpaceae-Dipterocarpoideae, 14.
Gramineae, *Aristida purpurea*, 22; *Bouteloua curtipendula*, 23; *Poa pratensis*, 24.	Ranunculaceae, *Caltha palustris*, 7.	Hydrophyllaceae, *Phacelia*, 6.			Sonneratiaceae, *Sonneratia*, 17.	Gramineae-Deschampsiinae, 21.
Hydrophyllaceae, *Phacelia corymbosa*, 6; *P. imbricata*, 6; *P. mutabilis*, 6; *P. nemoralis*, 6.	Rosaceae, *Sanguisorba minor*, 8; *S. officinalis*, 8.	Plantaginaceae, *Plantago*, 12.				Meliaceae, 20.
	Rubiaceae, *Oldenlandia corymbosa*, 9.	Polemoniaceae, *Phlox*, 13.				
	Scrophulariaceae, *Digitalis ambigua*, 3; *D. lanata*, 3; *D. lutea*, 3.					
	Solanaceae, *Datura stramonium*, 2; *D. tatula*, 2; *Nicotiana silvatica*, 2; *N. trigonophylla*, 2.					
	Umbelliferae, *Sanicula crassicaulis*, 10.					

References:
1. Gadella, 1964
2. Maurizio, 1956
3. Schwanitz, 1950
4. Kessler & Larson, 1969
5. Bronckers, 1963
6. Heckard, 1960
7. Smit, 1968
8. Erdtman & Nordborg, 1961
9. Lewis, 1964
10. Bell, 1954
11. Gould, 1957
12. Bassett & Crompton, 1968
13. Taylor & Levin, 1975
14. Muller, 1979
15. Lewis & Szweykowski, 1964
16. Pandey, 1971
17. Muller, 1969
18. Raj, 1961
19. Leuenberger, 1976
20. Pennington & Styles, 1975
21. Albers, 1975
22. DeLisle, 1970
23. Kapadia & Gould, 1964
24. Nissen, 1950

TABLE 2. Influence of external factors on pollen size.

Environmental Factors	+ Correlation	No Correlation
Light Intensity	Fagaceae, *Castanea*, 1.	
Temperature	Compositae, *Xanthium*, 2. Solanaceae, *Lycopersicon*, 2.	
Temperature and Humidity		Begoniaceae, *Begonia*, 7. Gesneriaceae, *Saintpaulia*, 7. Labiatae, *Coleus*, 7.
Water	Lythraceae, *Lythrum*, 3. Umbelliferae, *Sanicula*, 4.	
Root Crowding	Umbelliferae, *Sanicula*, 4.	
Mineral Nutrition	Alliaceae, *Allium*, 4. Compositae, *Helianthus*, 4. Cruciferae, *Sinapis*, 4. Cucurbitaceae, *Citrullus*, 4. Fagaceae, *Nothofagus*, 5. Gramineae, *Triticum*, 6; *Zea*, 4. Lythraceae, *Lythrum*, 3. Portulacaceae, *Portulaca*, 4. Solanaceae, *Lycopersicon*, 4; *Petunia*, 4. Umbelliferae, *Daucus*, 4.	

References:

1. Oner & Planchais, 1976
2. Kurtz & Liverman, 1958
3. Schoch-Bodmer, 1940
4. Bell, 1959
5. Harris, 1956
6. Wagenitz, 1955
7. Hebda & Lott, 1973

of the early Cretaceous angiosperm pollen types with indeed a simple morphology. It is only in the middle and late Cretaceous that larger, more complex pollen types start appearing. It appears probable that this increase in size was primarily caused by increased adaption to different systems of animal pollination.

However, transport conditions are not the only factors known to be correlated with pollen size. Also, level of polyploidy may express itself directly in pollen size, the higher the level the larger the grain. In Table 1, cases described in the literature are presented grouped according to taxonomic level. It is clear that the effect is most noticeable at the intraspecific level, less apparent at the interspecific level, while at the intergeneric level no correlation is known. This suggests that the influence of polyploidy on pollen size is minor, evolutionarily short-lived, and, apparently, easily overridden by quite different selective processes.

Some of the factors known to influence pollen size in the living plant are listed in Table 2, from which it is apparent that mineral nutrition is the single most important factor directly causing variation in pollen size. This fact is significant when considering Table 3 in which the correlation between flower characters and pollen vector with pollen size are listed. A first thing which is obvious is that, contrary to the evidence for correlation with ploidy level, no cases of intraspecific correlation are shown, but this is obviously a reflection of the rarity of intraspe-

TABLE 3. Relation of flower characters with pollen size.

	+ Correlation			No Correlation		
	A, Intraspecific	B, Interspecific	C, Intergeneric	A, Intraspecific	B, Interspecific	C, Intergeneric
Flower Size		Dipterocarpaceae-Dipterocarpoideae, 2. Fouquieraceae, 3. Fumariaceae, *Corydalis*, 1. Papaveraceae, *Meconopsis*, 1. Tamaricaceae, *Tamarix*, 4.	Dipterocarpaceae-Dipterocarpoideae, 2. Cactaceae, 10. Fumariaceae, 1. Polemoniaceae, 7. Sonneratiaceae, 6.		Solanaceae, *Nicotiana*, 9.	
Anther Length	Papaveraceae, *Platystemon californicum*, 1.	Papaveraceae, *Argemone*, 1; *Glaucium*, 1.				
Filament Length		Bromeliaceae, 5.				
Style Length		Polemoniaceae, *Phlox*, 6. Verbenaceae, *Glandularia*, 7.				Sonneratiaceae, 11. Verbenaceae, 12.
Fruit Size		Araliaceae, *Tetraplasandra*, 8.				
Pollen/Ovule Index		Solanaceae, *Nicotiana*, 9.				
Pollen vector Size			Polemoniaceae, 6.			Sonneratiaceae, 11.

References:

1. Layka, 1976a, 1976b
2. Muller, 1979
3. Henrickson, 1967
4. Baum, Bassett & Crompton, 1971
5. Ehler & Schill, 1973
6. Taylor & Levin, 1975
7. Schnack & Covas, 1945
8. Tseng, 1971
9. Pandey, 1971
10. Leuenberger, 1976
11. Muller, 1969
12. Covas & Schnack, 1945

cific differences in the characters listed. (The special case of stylar dimorphism has been excluded.) On the other hand, some clear cases of correlation at the intergeneric level in different families suggest that we deal here with important adaptive features.

For Dipterocarpaceae it has been argued (Muller, 1979) that the correlation between flower size and pollen size reflects differences in nutrient supply which are ultimately determined by selection for larger fruits. However, recent evidence (Ashton, pers. comm.) suggests that vector size may be involved also because, although the small-flowered Dipterocarpoideae are pollinated by thrips, the larger-flowered species are also visited by larger insects.

For the other cases listed of a possible correlation between flower size and pollen size, an explanation on the basis of different nutrition supply may also be the simplest one, but each case would have to be investigated in detail to rule out other causes. In *Tetraplasandra* (Araliaceae) Tseng (1971) has established a correlation with fruit size, comparable to the situation in Dipterocarpoideae. Although the correlation between pollen size and filament length reported for Bromeliaceae may be a similar phenomenon, the correlation between pollen size and style length falls in a different category altogether. This is because the style has to be penetrated by the pollen tube and this causes a built-in selective advantage for larger pollen grains with larger food reserves. Considering this, it seems surprising that only two cases of a positive correlation have been described, both at the interspecific level, while the cases of no correlation are probably more common than suggested. This emphasizes that genetic variability in size within a species may be limited by many other selective factors. In Sonneratiaceae, for instance, the genus *Duabanga* has much smaller pollen grains than *Sonneratia,* while style length is approximately equal. Moreover, both genera are bat-pollinated, hence absence of correlation with vector size. What is different, however, is the size of the flowers. In *Duabanga* the smaller flowers develop in more strongly branched inflorescences than is the case for the larger-flowered species of *Sonneratia*. This suggests, as for Dipterocarpoideae, the dominant influence of nutrition.

A relation between pollen size and vector size is indicated clearly only for Polemoniaceae. Although it is probable, as Heinrich & Raven (1972) have argued, that the energy balance of pollinators is partly affected by the amount and, presumably, size of the pollen gathered for food, it is perhaps more likely that the large showy flowers of these plants develop large pollen as a purely nutritional side effect. In fact, as Lee (1979) has pointed out, there may exist a close interrelation between flower size, style length, vector size, and pollen size.

A relation of a completely different character is shown by the pollen/ovule index and pollen size. For *Nicotiana* Pandey (1971) has found that self-compatible species or varieties of this genus have a lower ratio between the number of pollen grains and the number of ovules per flower than self-incompatible species and that the latter all have smaller pollen. Apparently, in self-compatible species fewer pollen grains are needed for fertilization, and, in consequence, more nutrients per pollen grain are available, leading to larger pollen size. Pandey (1971) also stressed that in *Nicotiana* pollen size is not directly related to chromosome number nor to size of flowers, and, in fact, the species with the largest flower

has small pollen grains. Reproductive economy thus appears to be the main determining factor here, and this may very well be of more general occurrence. It would be worthwhile to investigate this in more detail for related dioecious and monoecious species.

Still more different is the correlation with climate reported for *Ilex* by Lobreau-Callen (1975). In this genus, pollen size increases interspecifically both with altitude and latitude from which a correlation with climatic factors can be postulated. Earlier Cain & Cain (1948) reported a similar phenomenon for *Pinus echinata*. It would appear that even in these cases a nutritional phenomenon is involved, since the period of growth of the young pollen grains is generally correlated with the time a flower bud takes to develop which may very well be related to climate. A slow development would permit pollen grains to grow to a larger size. This hypothesis could be tested experimentally.

As this short survey demonstrates, a whole complex of different factors may have interacted to produce the often very specific and rather widely varying pollen sizes found within the angiosperms. Trends towards size increase in the fossil record may therefore be due to widely differing circumstances, although basically nutrition appears to be involved in most cases. The small size of many early Cretaceous angiosperm pollen grains is therefore most probably indicative of relatively small flowers.

The Wodehouse Effect

In the foregoing chapters an attempt was made to interpret exine morphology in terms of single characters such as apertures, size, or shape, but it will be evident that this is not really possible and that to be fully understood, the exine must be studied as a whole. To redress the balance, the following chapters will attempt to discuss the exine as an integrated morphological system, by evaluating some trends which affect more than one character.

The first discussion is based on the observation by Wodehouse (1935: 393) that the absolute size of a pollen grain influences harmomegathic functioning because of the fact that in solid bodies the volume is a function of the cube of the linear dimension, while the surface area is a function of the square of the same dimension. Moreover, the shape of a solid body also influences this ratio. Hence, according to Wodehouse, the ratio between volume and surface area may become reduced in smaller as well as in more elongated grains to such degree that exine elasticity by itself can accomodate the necessary changes in volume without the need for elaborate colpate harmomegathic structures. A larger grain would, in contrast, need a larger amount of harmomegathic space to accomodate a comparable volume reduction.

This effect, which is here termed the "Wodehouse effect" in honor of its discoverer, may very well have caused pollen-morphological trends in which size, shape, and apertures coevolved.

Wodehouse actually described its operation in connection with his detailed interpretation of the pollen types in *Polygonum*, but the same principle applies to other pollen types as well.

In general terms and starting from the sphere as the basic pollen shape, it

states that any increase in size needs a larger reduction in diameter to accomodate a given percent of volume reduction and hence more elaborate harmomegathic structures to accomodate the larger stresses.

Furthermore, for the same volume a change from a sphere to a more cylindrical, prolate shape needs a smaller reduction in diameter to achieve a given percent of volume reduction and therefore less elaborate harmomegathic structures to accomodate the smaller stresses. Thus the tricolpate harmomegathic system is better adapted to the prolate than to the spherical shape.

For the change from a sphere to a disclike, oblate shape, the same reasoning applies, except that colpate harmomegathic structures are, as already mentioned earlier, structurally less well adapted to this shape and are, in fact, often replaced by pores and other harmomegathic devices.

However, the Wodehouse effect may to a certain degree be counterbalanced by the relation existing between evaporation rate and volume, the smaller spherical grains evaporating relatively more rapidly than the larger grains and the prolate and oblate ones more rapidly than the spherical ones for the same volume. It obviously depends on the sealing properties of the exine how far this second principle counteracts the Wodehouse effect. In a case like Dipterocarpoideae, where the harmomegathic structures of the larger grains are strikingly similar to those of the smaller ones, it would seem that the Wodehouse effect has not resulted in any change in these structures because of this counterbalancing effect, the larger grains being less liable to suffer damaging water losses. In a case like *Polygonum*, as described by Wodehouse, efficient lipid sealing may have decreased the difference caused by the ratio volume/evaporation rate to such an extent that the Wodehouse effect has been a dominant factor in the evolution of the various pollen types. Of course, to demonstrate these interactions would involve precise measurements of transpiration rates, elasticity of the exine, and presence of sealing layers, and Payne (1972) has made a first attempt in this direction. The present discussion is therefore mainly intended to draw the attention of pollen morphologists to the theoretical possibility that these physical constraints may in certain cases have guided the integrated evolution of size, shape, and harmomegathic structures.

BREVIAXY

Van Campo (1966, 1976) has discussed in detail this widespread tendency for a spherical grain to develop towards a disc-shaped oblate type, caused by a relative shortening of the polar axis. If this spherical grain would be tricolpate and there would be no change in aperture condition, this would result in a considerable change in the distribution of harmomegathic stresses, as already mentioned earlier. Equatorial infolding of the colpi becomes more difficult and changes in volume will be more easily absorbed by overall changes in shape by shortening or lengthening of the polar axis, the equatorial belt acting as a hinge zone. This transference of function is probably the basic cause of the commonly observed reduction of ectoapertures. In other cases the ectoapertures become thin and superficial and tend to fuse at the poles (syncolpate condition) which permits only a limited amount of infolding, with stresses more equally distributed

over the polar hemispheres. In both cases a change from a circular towards a triangular outline accompanies the apertural changes. In case of concomitant reduction of ectoapertures the apertural corners tend to become rigid, while volume reduction mainly takes place both by shortening of the polar axis and by invagination of the mesocolpia.

In the case of *Tilia* pollen, although typically breviax, this process is not as yet far advanced. The circular equatorial outline shows infolding around the very much reduced ectoapertures. The pronounced collarlike strengthening of the endoapertures may prevent rupture when infolding is too strong. The exine architecture is uniform.

In *Plagioscyphus* (Sapindaceae, Fig. 6) the interapertural outline becomes concave in the shrunken condition, and the annulate endoapertures have become rigid areas, while the harmomegathic movements have been mainly restricted to the interapertural areas where exine differentiation has taken place. Clearly, compared to *Tilia* a more specialized system of harmomegathic functioning has evolved.

The architecture of *Bombax* pollen is again different. Here the ectoapertures have shortened but are not reduced as in the preceding types and have an interangular position. They are surrounded by a heavy reticulate exine pattern, clearly reinforcing the apertures and preventing infolding. In contrast, the interapertural areas have a thin flexible exine which accommodates harmomegathic movements.

Within the breviax trend these three pollen types thus represent different ways of harmomegathic functioning, in which shape, apertures, and exine architecture are closely integrated.

Longiaxy

In the longiax modification of the basic spherical shape the polar axis is elongated relative to the equatorial diameter, leading generally to more or less spindle-shaped prolate grains. The very widespread occurrence of this type as well as its early origin are probably due to the fact, mentioned before, that the tricolpate apertural system is best adapted to the longiax shape. Nevertheless, secondary modifications in shape, apertures, and exine structure do occur.

One interesting shape modification is the equatorial constriction leading to a dumbbell-shaped grain. This is well known from Umbelliferae (Cerceau-Larrival, 1967), but it occurs also, more rarely, in other unrelated families. One such case is the genus *Diplopeltis* (Sapindaceae) in which it only occurs in *D. huegelii*, the other species having developed a different shape and exine structure (Fig. 7). Basically this type represents a transfer of harmomegathic functioning from the colpi to the equatorial belt where exine thickness also has become reduced. In *D. huegelii* ectoapertures are not reduced, in contrast to most dumbbell-shaped umbelliferous pollen grains.

Very different modifications of the longiax shape are present in the fossil genus *Aquilapollenites*, in which a long polar axis is combined with protruding pores and reduced colpi. Here, the meridionally oriented harmomegathic areas appear to have been shifted to an intercolpate position, the pores acting, as in some breviax types, as rigid areas.

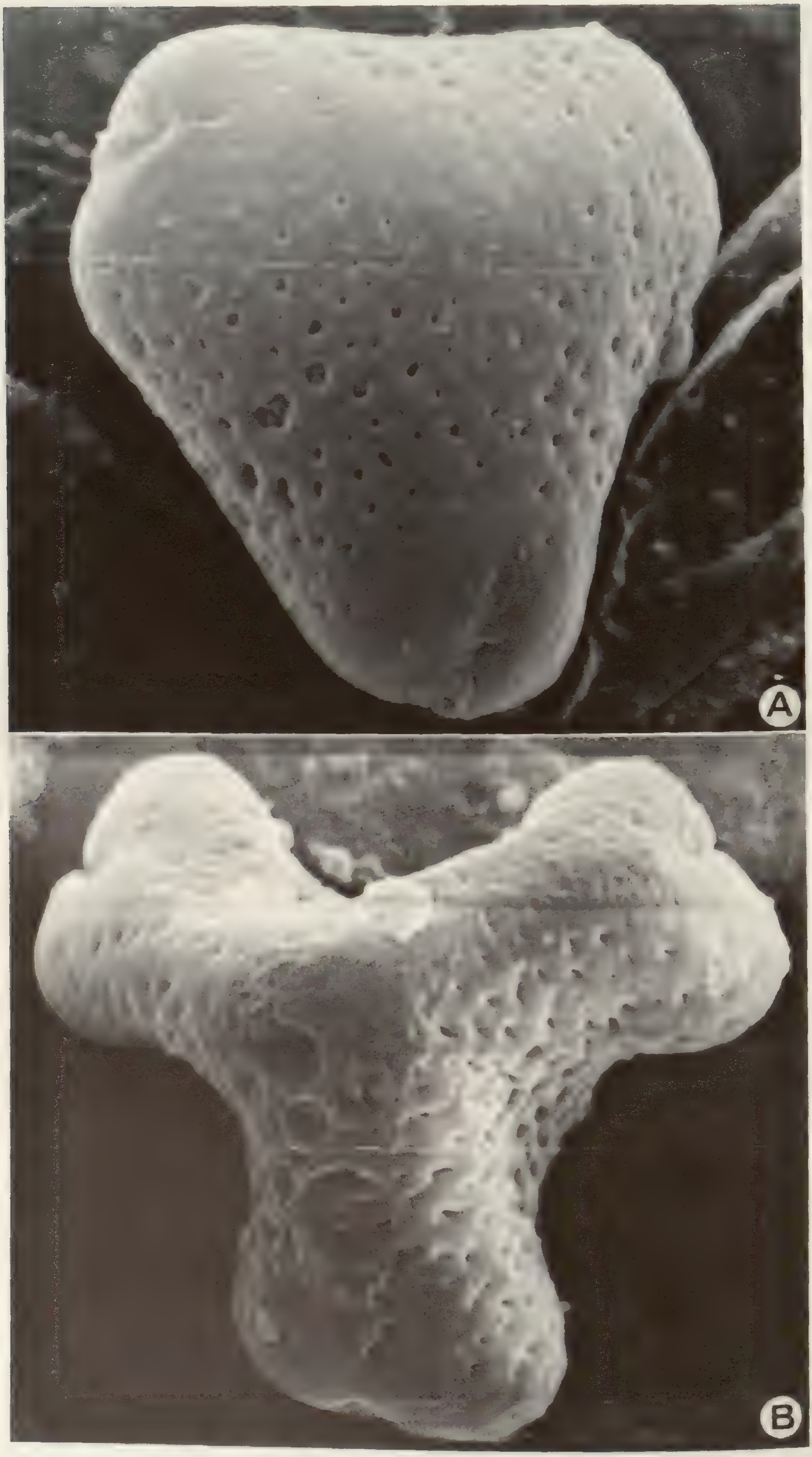

FIGURE 6. *Plagioscyphus nudicalyx* (Sapindaceae).—A. Expanded grain showing the triangular shape and rounded apertural corners with short, narrow colpi and the relatively large and scattered lumina on the equatorial part of the mesocolpia, decreasing in size towards poles and apertures. SEM.

FIGURE 7. *Diplopeltis* (Sapindaceae).—A. *D. eriocarpa*. Spindle-shaped pollen grain showing long, distinctly invaginated colpi without any exterior differentiation at the site of the endoapertures and with a slightly coarser exine structure on mesocolpia. SEM, acetolyzed, 2,500×.—B. *D. huegelii*. Dumbbell-shaped pollen grain with rather rigid polar areas due to thickened exine and more flexible equatorial belt with a loosely structured exine. The fairly long colpi show only a moderate amount of invagination. SEM, acetolyzed, 3,300×.

TRENDS IN TECTUM PATTERNS

The question whether the architecture of the tectum has any special functional significance has already been reviewed in general terms before. In this chapter its relation to the possible harmomegathic functioning of the entire exine will be discussed.

The earliest Cretaceous tricolpates, dating from the Aptian (zone C-VII of Doyle et al., 1977), are characterized by a uniform reticulate tectum, and this type still persists in families such as Menispermaceae, Dilleniaceae, and Flacourtiaceae. However, only slightly later in the Aptian (zone C-IX of Doyle et

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acetolyzed, 3,100×.—B. Contracted grain, showing invaginated mesocolpia with partly closed lumina while apertural areas have remained rigid due to endexinous thickenings. The short colpi are hardly invaginated. SEM, acetolyzed, 4,300×.

al., 1977) a differentiation starts between more coarsely reticulate mesocolpia and finer reticulation alongside the colpi. A similar differentiation takes place simultaneously in the reticulate monocolpate pollen group leading to the first recognizable monocotyledonous pollen types (Doyle, 1973). Since these changes generally involve also a differentiation in exine thickness, the more coarsely reticulate zones having a thicker exine, it would appear that this could be interpreted as an increase in harmomegathic efficiency. The primary folding function of the aperture membranes are thus extended to the bordering tectal zones which gradually change from thin, flexible marginal areas to the more rigid central mesocolpia. The widespread occurrence of this pollen type in many angiosperm families testifies to its effectiveness in controlling harmomegathic movements in this way.

A second type is the striate pattern also found very early in angiosperm history (zones C-VIII and C-IX, Aptian of Doyle et al., 1977). It is widespread in families such as Anacardiaceae, Leguminosae, Sapindaceae, and Burseraceae. Here the tectum is essentially transformed into a ridged sheet, which causes folding to be forced in one direction. Characteristically this pattern remains uniform and associated with uniform exine thickness. In prolate grains the ridges tend to be meridionally oriented in harmony with the colpate direction of folding. Ridges tend to fuse in poleward direction as the mesocolpia become more narrow, but it is interesting that there is generally no equivalent symmetrical fusion at the poles, but that the ridge systems of two mesocolpia fuse, the third abutting more or less at a right angle (Fig. 8B). This situation which probably reflects ontogenetic processes, presumably under tapetal influence, causes a certain asymmetry in the stress pattern.

The difference in degree of development of the striate pattern between the two closely related subspecies of *Litchi sinensis* (Sapindaceae), shown in Fig. 8, probably reflects stages in the evolution from a basically reticulate tectum towards a finely striate one.

It appears that in breviax grains the striate pattern is less frequent. In *Talisia* (Sapindaceae) the subprolate tricolpate pollen type is striate, while the oblate one with reduced colpi has a smooth tectum (Muller & Leenhouts, 1976).

In *Allophylus* (Sapindaceae) which has oblate-triporate pollen, striate patterns occur in a minority of types, mainly in Southeast Asia, and here the ridge pattern often becomes concentric around the apertural areas as a tubular strengthening, while at the poles a more irregular, but not clearly asymmetrical pattern develops (Fig. 9).

Allophylus cobbe is macromorphologically highly variable which is partly correlated with ecology (Leenhouts, 1967), but the pollen-morphological variation in tectum pattern shown in Fig. 10 is not correlated and appears to have evolved

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FIGURE 8. *Litchi sinensis* (Sapindaceae).—A. Subsp. *javensis*. Oblique equatorial view showing meridional orientation of striae at the margins of the colpi, while on the mesocolpia a more irregular orientation is present. The small isodiametric lumina visible between the ridges indicate that the ridges have probably developed over a finely reticulate tectum. SEM, acetolyzed, 5,000×.—B. Subsp. *philippinensis*. Polar view showing a dense, finely striate pattern, meridionally oriented but with asymmetric fusion of ridges at the pole. SEM, acetolyzed, 5,000×.

A
B

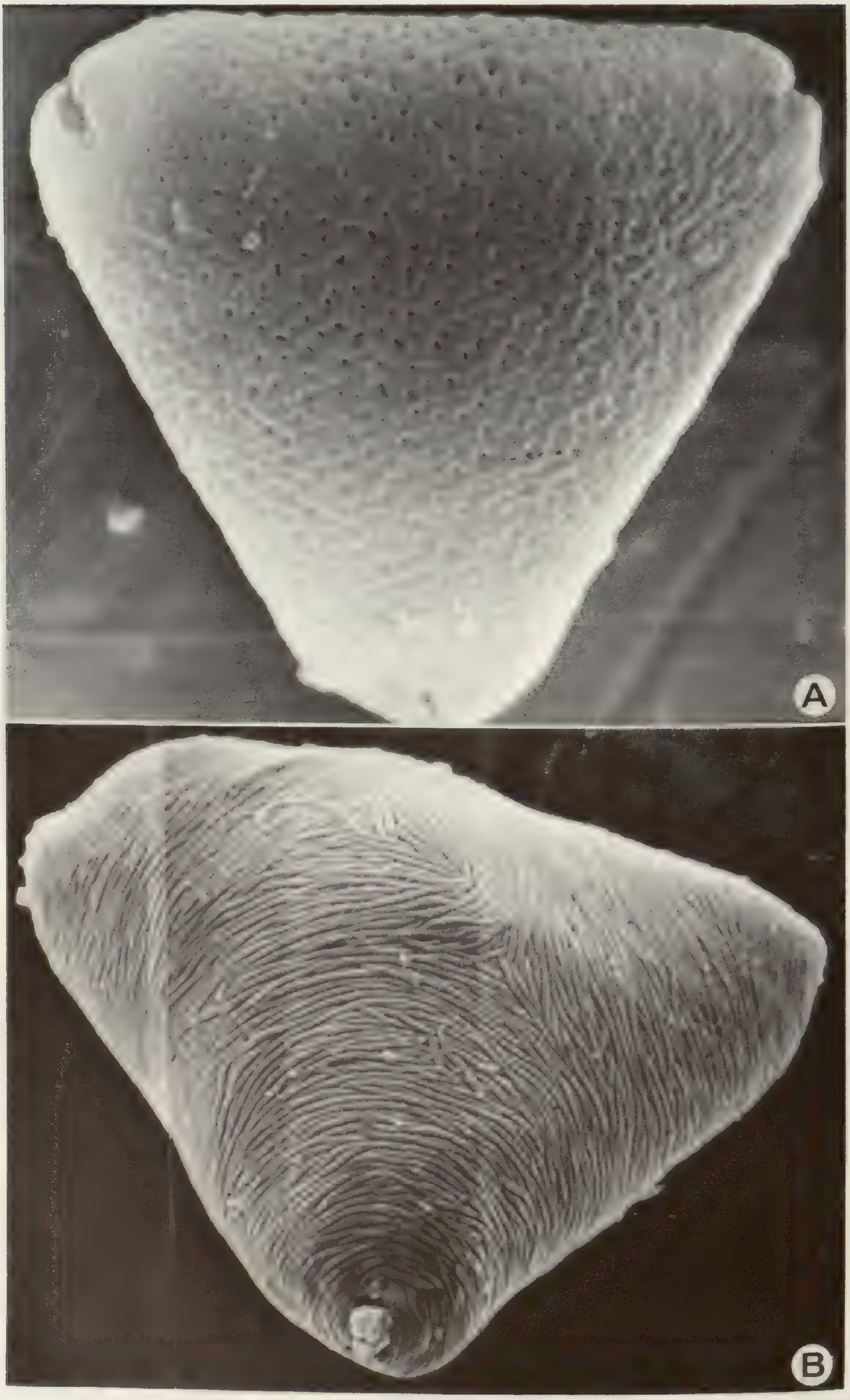

FIGURE 9. *Allophylus cobbe* (Sapindaceae).—A. Uniformly finely reticulate pollen type in polar view, small, irregularly porate-colpate apertures. *Dequaire 27678*, Madagascar. SEM, acetolyzed, 4,300×.—B. Finely striate pollen type in oblique polar view showing porate apertures with concentrically arranged striate pattern. Slightly irregular fusion of ridges at poles. *Kostermans 807*, Thailand. SEM, acetolyzed, 3,700×.

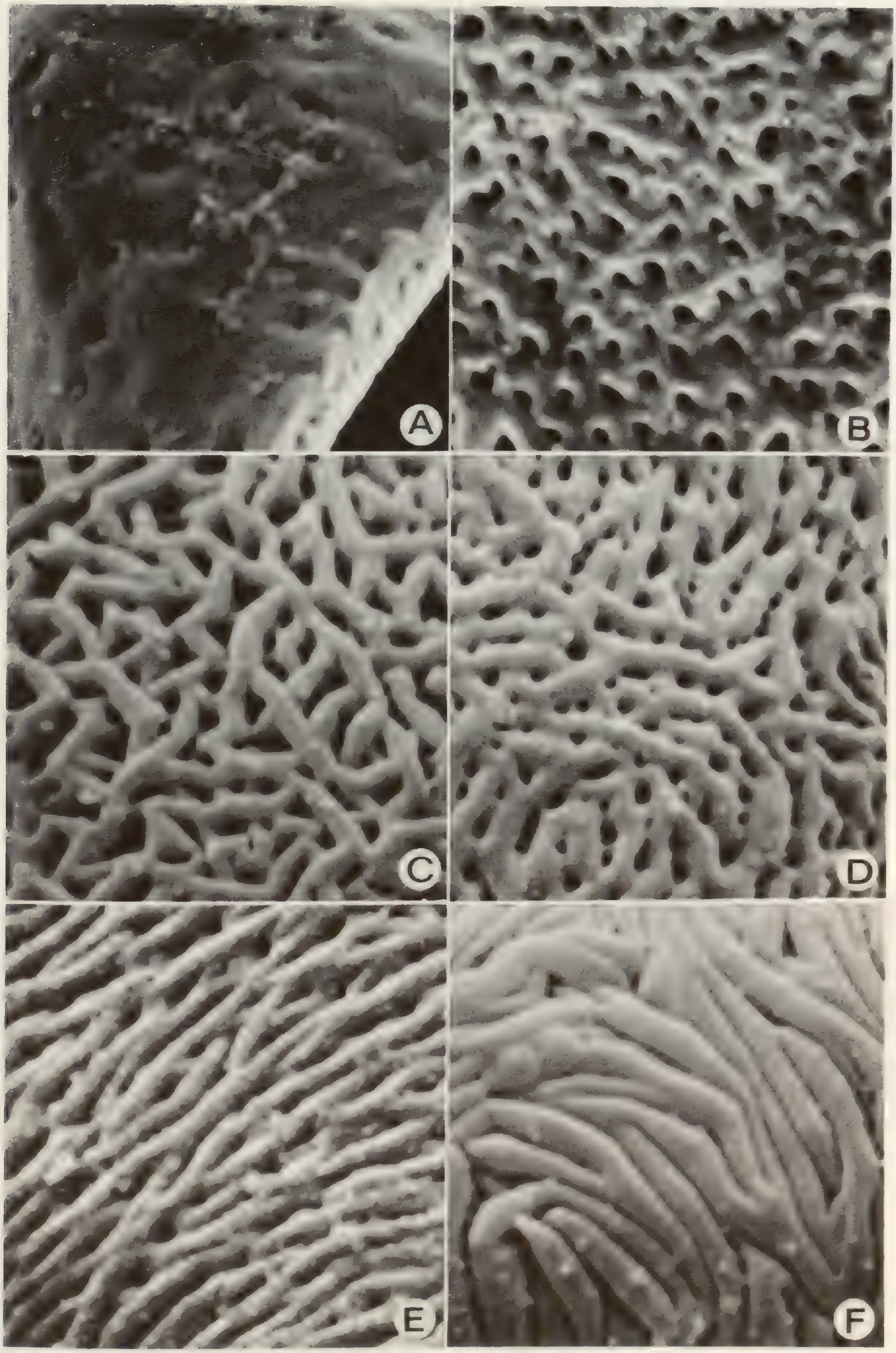

FIGURE 10. *Allophylus cobbe* (Sapindaceae), tectum patterns.—A. Nearly smooth, with scattered perforations. Section of exine shows sole, very short columellae and tectum. Rare, restricted to Sumatra and Borneo. *Korthals* s.n., Sumatra.—B. Finely reticulate. Restricted to Madagascar, New Guinea, and Pacific islands. *LB 12002*, Madagascar.—C. Retirugate. Restricted to South America. *Hassler 12231*, Paraguay.—D. Striate-reticulate. Dominant type occurring in all areas. *King 351*, Andamans.—E. Finely striate. Restricted to Southeast Asia. *Rabil 42*, Thailand.—F. Coarsely striate. Very rare, only found in Viet Nam. *d'Alleizette 1919*, Viet Nam. SEM, acetolyzed, 10,000×.

quite independently. The different patterns are difficult to understand other than as different structural solutions to stress absorption.

The functional significance of a third basic tectal structure, the Crotonoid pattern, which is also known to emerge very early in the fossil record (*Stellatopollis*, probably Barremian, cf. Doyle et al., 1977) is more difficult to interpret, although it may be considered a system of excrescences which upon volume reduction achieves efficient closure around porelike structures. Its apparently independent evolution in unrelated angiosperms suggests at least some adaptive advantage. It is remarkable, however, that the pseudocrystalline aspect of this structure is matched in the rigid wall patterns of certain tripylean Radiolaria.

A closed, smooth-surfaced tectum appears to be in many cases a secondary modification, especially in wind-pollinated species. However, in *Lepisanthes* (Sapindaceae), the breviax pollen type of *L. tetraphylla schizolepis* has evolved a very thin, flexible psilate exine over the harmomegathic areas, in contrast to the related *L. fruticosa* in which the reticulate ectexine is considerably thickened on the mesocolpia, accentuating the meridional folding of the colpi. Both species are insect pollinated (Muller & Leenhouts, 1976).

In the cases discussed here the tectal architecture is clearly integrated with aperture type and shape into a structure which allows maximum harmomegathic movement with a minimal chance of rupture of the exine.

PERISTASY

The term peristasy refers to a trend which develops from the basic tricolporate pollen type by reduction of ectoapertures and concomitant changes in exine structure towards a uniform distribution of harmomegathic forces over a sphere (from the Greek: peri = all around; stasis = rigidity).

Although structurally the peristatic type resembles the peri-aperturate end product of the successiform series, it differs strikingly in the ectoapertural reduction, and it could perhaps best be described as a disruption of the trend towards combination of ecto- and endoapertural functions in one structure. The disappearance of the meridionally oriented colpate folding structures is accompanied by the development of a more uniform reticulate pattern. The ectexine thickness and coarseness of the reticulum generally increases also. The endoapertures may persist underneath the reticulate ectexine, and the grains are then called cryptoporate. This trend is demonstrated for the genus *Harpullia* (Sapindaceae) in Fig. 11. A similar trend is apparent in Flacourtiaceae (*Hydnocarpus*, Schaeffer, 1972), Icacinaceae (*Gonocaryum*, Lobreau-Callen, 1972), Bignoni-

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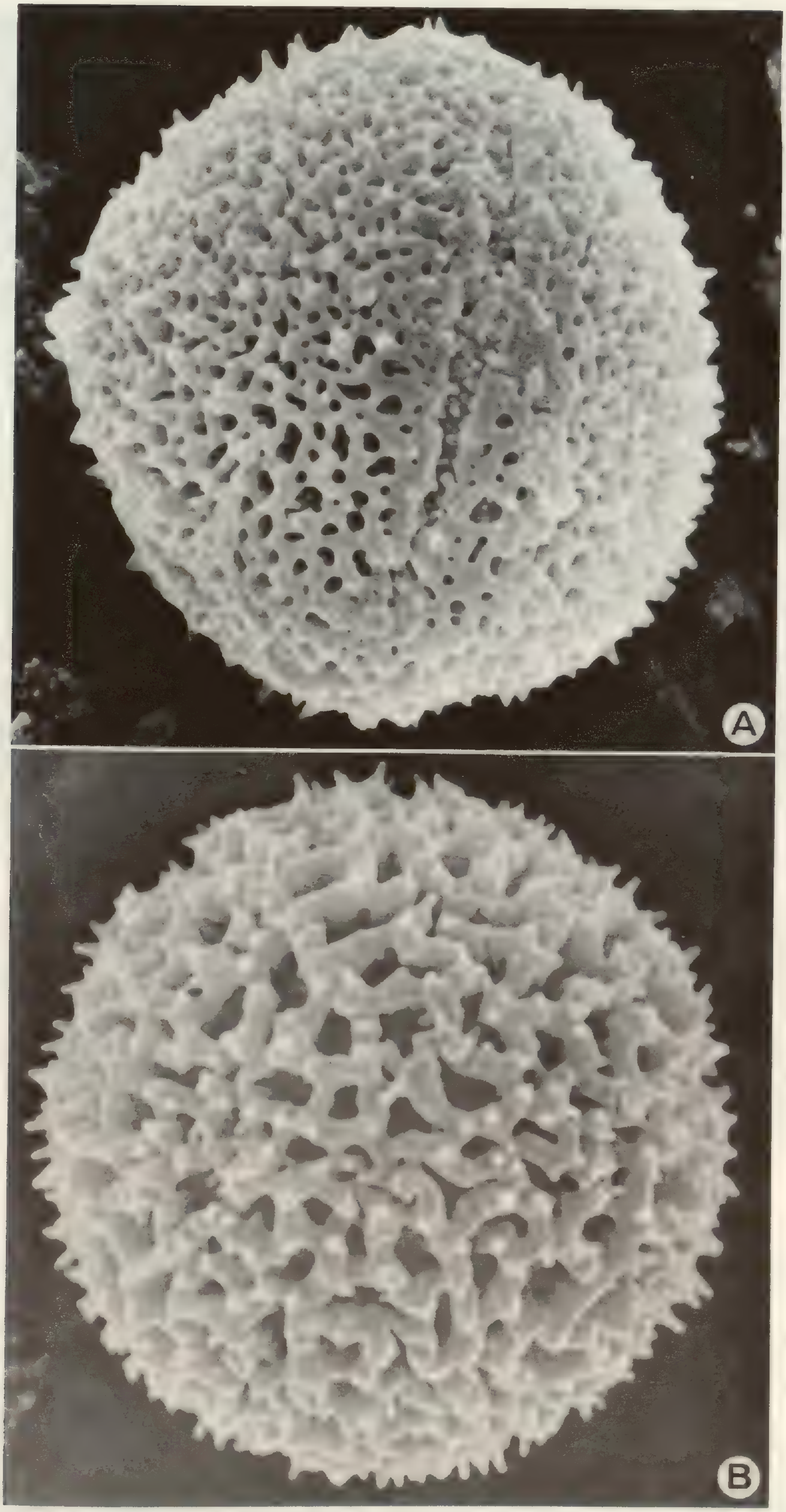
FIGURE 11. *Harpullia* (Sapindaceae).—A. *H. alata*. Equatorial view showing the relatively short, colpate ectoaperture, closed by a membrane which is covered with small spinules, without any clear indication of the endoapertures situated underneath. Tectum rather finely reticulate-echinate, slightly finer along colpus margins. *NSW 136084*, Australia. SEM, acetolyzed, 4,400×.—B. *H. crustacea*. Acolpate, endoapertures entirely hidden (cryptoporate). Tectum uniformly coarsely reticulate with broad ridges and heavy columellae, thus able to distribute harmomegathic stresses equally over the surface of this perfectly spherical grain (peristasy). *NGF 11839*, New Guinea. SEM, acetolyzed, 5,100×.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aceae (*Pithecoctenium,* Buurman, 1977), Dichapetalaceae (*Dichapetalum timoriense,* Punt, 1975), and Loganiaceae (*Fagraea,* Punt, 1978).

For Compositae, Wodehouse (1935) had already drawn attention to the demobilization of furrows and the transfer of the harmomegathic function to the enlarged pores in the lophate liguliforae-pollen type. Basically this is also a peristatic structure, in which the heavy cristae distribute stresses equally over the spherical surface providing an outer rigid structure, comparable to a geodesic dome. Within this structure, as recently discussed by Bolick (1978), the inner endexinous hull and the porate apertures are free to expand or contract according to the state of desiccation of the protoplasm.

Also the pollen grains of *Persicaria* can be considered peristatic. As Wodehouse (1935: 392) already pointed out, the elaborate reticulate system of high ridges imparts a stiffness to the exine, and furrows have disappeared. However, in this case pores have become more numerous, and on this aspect the pollen type might also be assigned to the successiform series.

FLEXIBLE EXINES

In contrast to the trend towards a stiffened exine, a trend towards extreme flexibility of the exine can be distinguished. Wodehouse (1935: 392) already recognized this basic structural design in anemophilous members of Polygonaceae (*Rumex, Rheum, Muehlenbeckia*), in which the colpi are reduced to long linear grooves with negligible width, even when expanded, and which have retained small endoapertures. The exine is relatively thin and finely and uniformly reticulately structured, while the shape is approximately spherical. When drying out, the colpi act as hinges and the thin, flexible exine follows the shape of the shrinking protoplast. An essentially similar structural principle characterizes certain Dipterocarpaceae (*Dryobalanops, Dipterocarpus,* cf. Maury et al., 1975). As shown in Fig. 4G, here also the colpi are long and narrow, and the exine is thin, without endexine and uniformly structured. However, the ectexine is not reticulate but, as pointed out before, has evolved into a peculiar urn-shaped tilioid pattern in which tectum and columellae are fused into a structural design which permits bending in all directions. This flexibility is, moreover, enhanced by the absence of the endexine and the reduction of the sole to a thin, lamellated basal layer. Also, in *Rumex acetosella* pollen a similar reduction to a basal, lamellar layer appears to have taken place (Nilsson et al., 1977).

For Polygonaceae, Wodehouse (1935) supposed this pollen type to have evolved in relation to anemophily, but in the dipterocarp genera mentioned, which are insect pollinated, this is unlikely. It appears more probable that in both cases the development of this specialized pollen type reflects a unique solution to harmomegathic stress accommodation.

This case demonstrates how in taxonomically distant families functionally similar pollen types have evolved, with a similar aperture structure and a reduced, but in detail significantly different exine architecture.

LATISTASY

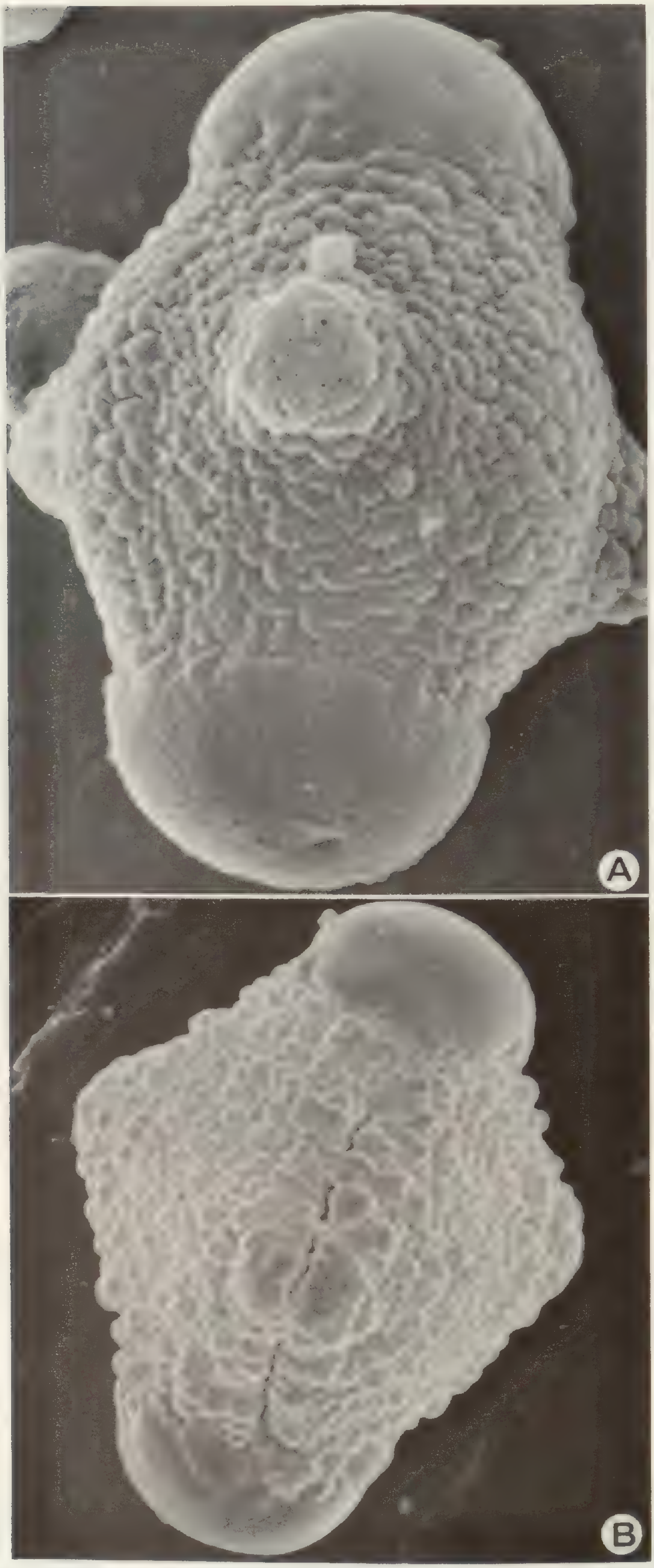
This term is introduced for pollen types in which the harmomegathic stress distribution pattern is latitudinally oriented. The most typical examples are the equatorial costae bordering the encircling endopertures in certain species of

FIGURE 12. *Xanthophyllum bullatum* (Polygalaceae). Oblique polar view showing the relatively smooth-surfaced polar cap, the short colpi with characteristically rounded tips and widening at the equator but without any possibility for invagination due to endexinous costae bordering the broad, equatorial-encircling endoaperture. The mesocolpia are thin over the endoaperture, effectively separating the pollen grain in two rigid halves, connected by flexible strips of exine which act as the main latitudinally oriented harmomegathic structures (latistasy). SEM, acetolyzed, 4,000×.

Utricularia (Lentibulariaceae), *Xanthophyllum* (Polygalaceae), and *Rhizophora* (Rhizophoraceae, Muller & Caratini, 1977).

In the case of *Xanthophyllum* (Fig. 12) the colpi do not act as folding structures and the volume accommodation appears to have been entirely transferred to the flexible strips of mesocolpia connecting the rigid polar areas.

In *Rhizophora* the three colpi may be more or less distinctly developed, according to the species, but they appear not to act as folding structures. In *R. racemosa* they are most strongly reduced, while the shape has become suboblate, and the polar area appears to be more flexible in comparison to the spherical grains of *R. mucronata* which have a thickened polar exine with a microreticulate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B

structural differentiation. Thus *R. racemosa* pollen appears to be more advanced in the trend towards latistasy than the pollen of the other species of the genus.

In the pollen grains of *Sonneratia caseolaris* a latistatic structure is apparent, as shown by the latitudinal hinge line separating the rigid, smooth, and thick polar cap from the more flexible verrucate equatorial belt (Muller, 1978). It is of interest that an essentially similar pollen type has been described by Nowicke & Skvarla (1974) in *Tournefortia,* pollen type II. The two pollen types are compared in Fig. 13 and show a remarkable correspondence in shape and sculptural distribution but differ in the presence of reduced ectocolpi in *Tournefortia*. In ultrastructure there is also correspondence in the thick endexine over the equatorial belt which rather abruptly becomes very thin over the polar area, but the structure of the ectexine at the poles again differs slightly. Nowicke & Skvarla (1974) could find no relation between pollen types and environment or pollination vector in *Tournefortia,* while also in *Sonneratia* the different pollen types can not be related to environmental factors. The convergent development of a highly specialized, functionally comparable pollen structure in such taxonomically widely separated genera is therefore an indication that factors relating to harmomegathic efficiency may have been at work.

Conclusions

The preceding discussion shows, for a few selected examples, how far exine morphology can be understood as a result of different processes. Primary are the limitations imposed by the physicochemical process of sporopollenin deposition, the induction of apertures, and growth processes. These are the nomothetical aspects of form development referred to by Van Campo (1976). Next are the inherited structures such as colpi which may be changed or eliminated in the evolutionary process if their function changes or is transferred. Finally there is the innovative aspect leading to new structures such as endoapertures, spines, and novel harmomegathic systems.

In general pollen morphology follows the principle of evolutionary canalization (Stebbins, 1975). This is based on conservation of organization, causing preservation of structures already evolved and only slow modification without inadaptive intermediate stages and adaptive modification along the lines of least resistance. These changes are more likely to occur because they are based on the smallest possible number of gene substitions.

This explains why, once a certain adaptive level such as peristasy, the heterocolpate condition, breviaxy with syncolpy, or the triporate condition has been reached, further development is more likely to lead to further refinements than to radically new types. In Lecythidaceae, for instance, once the syncolpate type

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FIGURE 13.—A. *Sonneratia caseolaris* (Sonneratiaceae). Equatorial view showing protruding pores covered with irregularly verrucate exine, absence of ectoapertures, densely verrucate equatorial belt and smooth polar caps. SEM, acetolyzed, 2,470×.—B. *Tournefortia hispida* (Boraginaceae). Equatorial view showing protruding pores covered with large verrucae, separated by narrow colpate ectoapertures which can invaginate only in a limited way, densely verrucate equatorial belt and smooth polar caps. SEM, acetolyzed, 3,750×. Courtesy Dr. J. Nowicke.

originated, further development appears to have been canalized into refinements in aperture construction (Muller, 1973).

To this, the principle of transference of function, as stated by Corner (1958), should be added. It appears to have been operative in some of the cases of harmomegathic adaptations cited in this paper.

Although many aspects of exine morphology, especially those connected with the reservoir function, still defy analysis, it has nevertheless become clear that the pollen wall represents a highly complex system in which many different and often temporally spaced functions are closely integrated. The large variability of angiosperm exine morphology probably reflects compromises between the different functional aspects, often with one function dominating. This will depend primarily on the ecological situation but will then often lead to evolutionary canalization of structural development.

This interpretation is of importance when exine characters are utilized in taxonomy. Structural features should be evaluated within the general adaptive context, and this is especially important in numerical approaches to palynotaxonomy (Hideux, 1977), which run the risk of overestimating the number of truly independent exine characters.

Also, the recognition of separate morphological trends as a base for taxonomic evaluation (Punt, 1976) should be complemented by a consideration of functional interdependence. This is especially important for recognition of the many striking convergences which are so widespread in angiosperm pollen types.

Finally, the interpretation of the fossil pollen record can be considerably broadened if the structures preserved are interpreted in terms of function and ecological significance for the plant as a whole. Doyle (1977) has recently made a first attempt in this direction in his analysis of the morphological evolution of early Cretaceous angiosperm pollen types.

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POLLEN MORPHOLOGY: THE POTENTIAL INFLUENCE IN HIGHER ORDER SYSTEMATICS[1]

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ABSTRACT

The pollen of approximately 650 species from at least 25 families has been examined in LM and SEM, and a representative number in TEM. These families include those found in the orders: Centrospermae, Plumbaginales, Polygonales, Primulales, Ranunculales, and Dilleniales. Evidence from pollen morphology: reinforces the close tie between the betalain families and the Caryophyllaceae and Molluginaceae; confirms the exclusion of the Batidaceae, Gyrostemonaceae, and Theligonaceae from the Centrospermae; dismisses any close relationship between the Centrospermae and the Plumbaginaceae, Polygonaceae, or Primulaceae; eliminates the possibility of a close relationship among Plumbaginaceae, Polygonaceae, or Primulaceae; would not support a close relationship among the families in the Order Ranunculales; suggests that the Ranunculaceae may be the closest extant relative of the Centrospermae; supports separate family status for *Berberis* and *Mahonia*; indicates that most of the remaining berberidaceous genera are best treated as one family; should be regarded as a critical or key characteristic for determining the position in the dicot hierarchy of Batidaceae, Gyrostemonaceae, and Corynocarpaceae, and, to a lesser extent, Theligonaceae.

The present system for the classification of the angiosperms is based primarily on floral morphology, and most families have been the subject of detailed studies, reexaminations, and even revisions. Over the last few decades the relationships of various taxa have been refined and clarified by the incorporation of data from sources such as cytology and phytochemistry. The information derived from palynological investigations has also had a limited influence, but the development of the scanning electron microscope (SEM) has revolutionized the study of surface structures by providing a depth of focus never possible in light microscopy. Palynologists now have the means to fully exploit the morphological characteristics of the male gametophyte with the attendant conservatism and stability associated with reproductive structures. The potential influence of pollen morphology on the classification of the angiosperms cannot be overemphasized; for the first time there is a parameter which is ubiquitous, the material readily obtainable (the vast herbarium collections of the world) and simple to prepare, and the resulting micrographs have great precision and a degree of uniformity that permits accurate comparison regardless of their source.

While the flower may indeed be ubiquitous to the angiosperms, the great proliferation and modification of each of the parts make it nearly impossible to utilize the principle of comparative morphology (i.e., similarity indicates relationships) unless the taxa are already considered related (some major specializations in common), and the question is the extent of relationship to each other.

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In the last ten years the SEM has revealed an almost unbelievable diversity of pollen morphology, but this variation does not have the complexities of floral morphology and the associated difficulties of interpretation.

This paper reviews the results from an extensive and continuing investigation that had its origins in delimiting the order Centrospermae, perhaps the most distinctive order in the flowering plants. At this writing, the pollen of 650 species has been examined and the list now includes the Plumbaginales, Polygonales, Primulales, Ranunculales and Dilleniales. The authors hope to demonstrate the value of pollen morphology—the nature of evidence, the interpretation, the implications—in assessing the relationships of large taxa, mostly families, to each other.

The organization of this article is as follows: orders Centrospermae s.l., Plumbaginales, Polygonales, Primulales, Ranunculales, and Dilleniales. The families within each of these orders will be described with reference to size, distribution, unusual characteristics of floral and/or vegetative morphology, and problematical genera. An overview of the pollen morphology of each of these families is presented: aperture type, tectum, and wall structure, with the range of variation in each, and distinguishing features, if any. Finally, the relationships of each family as indicated by the palynological data.

All pollen has been processed for light microscopy (LM), scanning electron microscopy (SEM), and transmission electron microscopy (TEM) by methods already described (Nowicke & Skvarla, 1977). All specimens studied are listed in Table 1.

THE ORDER CENTROSPERMAE

The order Centrospermae, which in the past has been circumscribed by a host of floral and embryological features, the most definitive being a curved embryo with a perisperm storage tissue, may well be the best example of a large natural association of families. The common morphological characteristics have, however, all been eclipsed by discoveries made at the chemical and ultrastructural levels.

Most of the red blue colors in the flowering plants are due to a general class of pigments, the water soluble anthocyanins, present in the cell vacuole. For the vast majority of the angiosperms the structure of the anthocyanin molecule varies only slightly. In the order Centrospermae, however, the molecule responsible for the red blue color is significantly altered by the incorporation of two (usually) nitrogen atoms. These N-containing pigments have been designated "betalains," after the genus in which they were first discovered, *Beta* L., in the Chenopodiaceae. The anthocyanins and the betalains never occur together in individual plants, different plants of a species, or families, etc.

The second discovery at the ultrastructural level was the existence of two types of sieve-tube plastids, starch or protein, with the former being the most common in the dicots. The Centrospermae have a unique protein type, a peripheral ring of fibrous protein and usually a central crystalloid (Behnke, 1976).

The discovery of the betacyanins and their gradual elucidation date back to the second half of the 19th century (see Dreiding, 1961, for review). The dean of American plant anatomists, Katherine Esau, appears to have been the

TABLE 1. Specimens examined, arranged alphabetically by family.

Taxa	Collector	Location	Figure	Pollen Description: Aperture, Tectum
ACHATOCARPACEAE				
Achatocarpus spinulosus Grisebach	Venturi 472	Argentina	59	4–6-porate, coarsely granular
AIZOACEAE (including Molluginaceae)				
Acrodon bellidifloris N. E. Brown	Van der Bijl 33 (K)	S. Africa		3-colpate, spinulose-perforate
Adenogramma galioides Fenzl	Rogers, F. A. 16132	S. Africa		3-colpate, spinulose-punctate
Aizoon hispanicum L.	Kocher B-237	Jordan		3-colpate, spinulose-punctate
Delosperma abyssinicum Schwantes	Gillett 13948 (K)	E. Africa		3-colpate, spinulose-perforate
D. ecklonis Schwantes	Brown s.n. 1/29/22 (K)	Oxford Bot. Gards.	23	3-colpate, spinulose-perforate
D. mahonii N. E. Brown	Galpin 1085 (K)	S. Africa		3-colpate, spinulose-perforate
Gisekia pharnaceoides L.	Kundu & Balakrishnan 361	Ceylon	1, 2, 37	3-colpate, spinulose-punctate
Macarthuria australis Hueg.	Shell Oil Co. USNH 1756519	Australia		3-colpate, spinulose-punctate
Pharnaceum incanum L.	Rogers 16737	S. Africa	16	3-colpate, spinulose-punctate
Sesuvium erectum Correll	Stearns 33	Texas		3-colpate, spinulose-punctate
S. maritimum Britt., Sterns & Pogg.	Killip 40932	Florida		3-colpate, spinulose-punctate
S. verrucosum Raf.	Wooton & Standley s.n. 9/15/07	New Mexico		3-colpate, spinulose-punctate
Tetragonia dimorphantha Pax	Werdermann & Oberdieck 2292	S.W. Africa		3-colpate, spinulose-punctate
T. pedunculata Phil.	Metcalf 30339	Peru		3-colpate, spinulose-punctate
T. vestita I. M. Johnston	Hutchison 1320	Peru	3, 4, 38	3-colpate, spinulose-punctate
AMARANTHACEAE				
Alternanthera flavescens H.B.K.	Killip 42415a	Florida	36	recessed pores, spinulose-punctate
Dicraurus leptocladus Hook. f.	Pringle 13604	Mexico		recessed pores, spinulose-punctate
Gomphrena brownii Moq.	White, C. T. 8658	N. Queensland		recessed pores, spinulose-punctate
G. elegans Mart.	Ochoa 540	Peru	29, 49	recessed pores, spinulose-punctate
Iresine angustifolia Euphr.	Dugand 5486	Colombia	30, 52, 53	recessed pores, spinulose-punctate
Pfaffia iresinoides (H.B.K.) Spreng.	Bro. Daniel 741	Colombia	35	recessed pores, spinulose-punctate
Tidestromia oblongifolia (S.Wats.) Standl.	Train 662	California		recessed pores, spinulose-punctate

TABLE 1. Continued.

Taxa	Collector	Location	Figure	Pollen Description: Aperture, Tectum
BASELLACEAE				
Basella excavata S. Ell.	Croat 32007 (MO)	Madagascar	22, 54, 55	6-colpate, deeply punctate
BATIDACEAE				
Batis maritima L.	Gaumer & Sons 23257	Yucatan	61	3-colporoidate, finely granular
	Jack 7178	Cuba		3-colporoidate, finely granular
	McAtee 3287	Georgia	69, 70	3-colporoidate, finely granular
	Stoddart 440	British Honduras		3-colporoidate, finely granular
BERBERIDACEAE				
Berberis fendleri A. Gray	Eastwood 5272	Colorado	138, 144	irregular, unspecialized
Diphylleia sinensis Li	Rock 4230	China	140, 148	3-colpate, spinose
Epimedium sempervirens Nakai	Masayuki Oue 33	Japan	143	3-colpate, small rods randomly distributed
Jeffersonia diphylla (L.) Pers.	Shafer & Miller 180a	Pennsylvania	142, 147	3-colpate, striate
Mahonia nervosa (Pursh) Nutt.	Belton s.n. 5-26-43	Oregon	141, 145	irregular, unspecialized
Podophyllum peltatum L.	Braun 3911	Kentucky	146	3-colpate, small rods randomly distributed
	McDougall 1231	Mississippi	139	3-colpate, small rods randomly distributed
CACTACEAE				
Opuntia lindheimeri Engelm.	Griffiths 9031	Texas	21, 57	large pores, reticulate
CARYOPHYLLACEAE				
Cometes surattensis L.	Rechinger, K. H. & F. 3247	Iran	17, 45	3-colpate, spinulose-punctate
Herniaria glabra L.	Staszkiewicz 527	Poland	24, 58	3 pores, spinulose-punctate
H. hemistemon J. Gay	Rechinger 8636	Iraq		pantoporate, spinulose-punctate
Paronychia canadensis (L.) Wood	Collins s.n. 7/12/31	Rhode Island		pantoporate, spinulose-punctate
	Fernald & Long 14325	Virginia		pantoporate, spinulose-punctate
P. fastigiata (Raf.) Fern.	Hartley & Peterson 7279	Wisconsin	31	pantoporate, spinulose-punctate
Sclerocephalus arabicus Boiss.	Mandaville 1251	Saudi Arabia	25	porate, spinulose-punctate
Siphonychia americana (Nutt.) T. & G.	Harper, R. 1696	Georgia		recessed pores, spinulose-punctate
	Thorne 15254	S. Florida	27, 50, 51	recessed pores, spinulose-punctate

TABLE 1. Continued.

Taxa	Collector	Location	Figure	Pollen Description: Aperture, Tectum
S. diffusa Chapm.	Wilbur & Webster 2660	Florida	26	recessed pores, spinulose-punctate
S. pauciflora Small	Brass 14469	Florida	33	recessed pores, spinulose-punctate
S. rugelii Chapm.	Thorne 6418	Georgia	32	recessed pores, spinulose-punctate
CHENOPODIACEAE				
Anabasis setifera Moq.	Mandaville, Jr. 3830	Saudi Arabia	28, 48	pantoporate, spinulose-punctate
Beta vulgaris L.	Bowden & Sims 1183	Balearic Islands	9, 10, 41, 42	pantoporate, spinulose-punctate
Halocharis clavata Bge.	Rechinger, K. H. 17312	Afghanistan		pantoporate, spinulose-punctate
Nitrophila occidentalis S. Wats.	Plumb 75	Arizona	34	pantoporate, spinulose-punctate
DIDIEREACEAE				
Alluaudia humbertii Choux	Decary s.n. 10/28/24	Madagascar	11, 12, 43	5–7 zonocolpate, spinulose-perforate
GYROSTEMONACEAE				
Codonocarpus attenuatus H. Walter	Vickery, J. s.n. 3-2-37	New South Wales	63	3-colpate, psilate
C. cotinifolius (Desf.) F. Muell.	Koch, M. 3021 (MO)	Merredin, W. A.	68	3-colpate, psilate
Didymotheca pleiococca F. Muell.	French, C. s.n. 1888	Australia	64	3-colpate, psilate
	von Mueller s.n. (MO)	Bordertown, S. A.	65, 66, 67	3-colpate, psilate
Gyrostemon australasicus (Moq.) Heimerl	Muir 1125	Australia	62	3-colpate, psilate
Tersonia brevipes Moq.	Morrison s.n. 10/8/00	Australia		3-colpate, psilate
NYCTAGINACEAE				
Boerhaavia erecta L.	Harrison & Kearney 8016	Arizona	7, 8, 40	pantoporate, spinulose-tubuliferous
Reichenbachia hirsuta Spreng.	Elisa 3154	Paraguay	20, 56	3-colpate, reticulate
Salpianthus arenarius H. & B.	Purpus 6693	Mexico	14, 44	3-colpate, spinulose-punctate
PHYTOLACCACEAE				
Phytolacca americana L.	Larsen 779	Delaware	46	3-colpate, spinulose-punctate
	McGregor, E. 342	Kansas	15	3-colpate, spinulose-punctate
Stegnosperma halimifolium Benth.	Collins et al. 186	California	18, 47	3-colpate, spinulose-punctate
PLUMBAGINACEAE				
Armeria maritima (Miller) Willd.	Mathiesen & Pedersen s.n.	Denmark	85, 86	3-colpate, coarsely reticulate

TABLE 1. Continued.

Taxa	Collector	Location	Figure	Pollen Description: Aperture, Tectum
	Svenson s.n.	Scandinavia	83, 84	3-colpate, finely reticulate
A. maritima var. *sibirica* (Turcz.) Lawrence	Cody 1794	Greenland	77, 78, 79	3-colpate, reticulate
	Calder 2014	Canada	80, 81, 82	3-colpate, reticulate
Ceratostigma griffithii C. B. Clarke	Rock 6577	China	71, 72, 89	3-colpate, pointed verrucae
	Rock 11578	China	73, 74, 90	3-colpate, rounded verrucae
Statice sinuata L.	Maire & Wilczek 1048	Morocco	87	3-colpate, finely reticulate
	Vaccari 495	Greece	88	3-colpate, coarsely reticulate
S. tenella Turcz.	Chaney 517	Mongolia	75	3-colpate, coarsely reticulate
	Chaney 517a	Mongolia	76	3-colpate, finely reticulate
POLYGONACEAE				
Atraphaxis spinosa L.	Rechinger, K. H. 16625	Afghanistan	95, 96, 118, 119	3 colporate, striate-punctate
Chorizanthe paniculata Benth.	Bro. Claude Joseph 2997	Chile	97, 120	3 colporate-punctate
Emex australis Steinheil	Seydel 2975	S.W. Africa	98, 122, 123	3 colporate, spinulose-perforate
Fagopyrum cymosum (Trev.) Meisn.	Stainton, Sykes, Williams 630	Nepal	92	3 colporate, deeply punctate
F. esculentum Moench	Braun s.n.	Ohio	116	3 colporate, deeply punctate
Koenigia islandica L.	Eyerdam 1601	Alaska	93, 94, 117	pantoporate, spinulose
Muehlenbeckia polybotryar Meisn.	Pritzel 399	Australia	91, 115	3 colporate, punctate-striate
Podopterus mexicanus H. & B.	Langlassi 922	Mexico	100, 121	3 colporate, microreticulate
Polygonum amphibium L.	Braun s.n. VI-29-12	Indiana	105, 112	pantocolpate, finely reticulate
P. cilinode Michx.	Hardin 722	N. Carolina	107, 111	3 colporate, finely punctate-striate
P. convolvulus L.	Horr & McGregor E495	Kansas	103, 109	3 colporate, psilate and spinulose
P. forrestii Diels	Rock 9697	China	104, 110	pantocolpate, spinulose
P. glaciale (Meisn.) Hook. f.	Stainton et al. 3872	Nepal	106	3-colpate, reticulate
P. orientale L.	Johnston s.n. 8/16/24	New York	108, 113	pantoporate, reticulate
P. vaccinifolium Wall.	Koelz 976	India	101, 114	3 colporate, punctate
Rumex scutatus L.	Pfister 1158/2	France	99	3 colporate, spinulose-perforate
Ruprechtia pallida Standl.	Newman 17	Mexico	102, 124	3 colporate, perforate-rugulose

TABLE 1. Continued.

Taxa	Collector	Location	Figure	Pollen Description: Aperture, Tectum
PORTULACACEAE				
Anacampseros filamentosa Sims	Rose & Stewart s.n. 1912	S. Africa		pantocolpate, spinulose-perforate
Ceraria fruticulosa Pears. & Steph.	Werdermann & Oberdieck 566	S.W. Africa	5, 6, 39	3 colporate, spinulose-punctate
Lenzia chamaepitys Phil.	Johnston 6091	Argentina	13	3-colpate, spinulose-punctate
Montia meridensis Friedr.	Hammen 1194	Colombia	19	pantocolpate, reticulate
PRIMULACEAE				
Anagallis linifolia L.	Reverchon 388	Spain	126, 133	3 colporate, prominently punctate
Coris monspeliensis L.	Tidestrom 13554	France	125, 131	3 colporate, sculptured and psilate
Cortusa matthioli L.	Koelz 4994	India	127, 135, 136	3 syncolporate, granular
Glaux maritima L.	Haakana s.n.	Finland	128, 132	3 colporate, punctate-striate
Naumbergia thyrsiflora (L.) Reichenbach	Andersen s.n.	Norway	129, 134	3 colporate, irregularly micro-reticulate
Primula officinalis (L.) Jacq.	Ludera s.n.	Poland	130, 137	5–8 zonocolpate, microreticulate
RANUNCULACEAE				
Adonis pyrenaica DC.	Salzmann s.n.	France	153, 158	3-colpate, spinulose-punctate
Anemone coronaria L.	Heldreich s.n. 12. 91.	Greece	149, 155	pantoporate, spinulose-punctate
Clematis orientalis L.	Raikova 2915	U.S.S.R.	152, 156	3-colpate, spinulose-punctate
Coptis occidentalis (Nutt.) T. & G.	Constance, Clements, Rollins 1065	Idaho	159	pantoporate, spinulose-punctate
	Sandberg 217	Idaho	151	pantoporate, spinulose-punctate
Eranthis hyemalis (L.) Salisb.	Javorka & Timko s.n. 3/1/11	Hungary	154	3-colpate, spinulose-punctate
Helleborus viridis L.	Livingston s.n. 27/3/66	England	164, 165	3-colpate, reticulate
Paeonia brownii Dougl.	Cronquist 6380	Oregon	160, 161	3-colpate, finely reticulate
Ranunculus muricatus L.	Koelz 14669	Iran	150, 157	pantocolpate, spinulose-punctate
Trollius acaulis Lindl.	Koelz 5046	India	162, 163	3-colpate, striate
THELIGONACEAE				
Theligonum cynocrambe L.	Pitard 263 (MO)	Tunesia	60	pantoporate, "reticulate"

first to detect the proteinaceous fibers in the sieve-tube plastids of *Beta vulgaris* L., in 1934. There is an apparent gap in the literature until 1964 when Falk reported this type in *Tetragonia expansa* Murr., from the Aizoaceae. But until examination of large numbers of taxa revealed the restricted distribution, the significance of these discoveries could not be fully appreciated (Behnke, 1975).

In fact, the extreme distinction of the order has been exploited by some phylogeneticists as evidence of a polyphyletic origin of the angiosperms. This may be overstating the case, but it would be difficult to refute the idea that the ancestral stock of the Centrospermae separated very early in time from the remaining angiosperms, certainly from the dicots. If the separation was later, then the large size of the order has been the result of rapid proliferation and this phenomenon is more difficult to explain.

Two families, the Caryophyllaceae and the Molluginaceae, which have been placed in the Centrospermae by various authors on morphological bases (Harms, 1934; Cronquist, 1968; Takhtajan, 1969), lack the distinctive betalain pigments. As a result, their placement has been the subject of some controversy.

When Behnke's (1969) investigations of sieve-tube plastids were extended to the Caryophyllaceae and Molluginaceae, he found that these two anthocyanin families had the peripheral ring of fibrous proteins that characterized the betalain families. Moreover, he was now able to distinguish three groups based on the central crystalloid: globular, the most common; polygonal, found in the Caryophyllaceae and in two other genera, *Limeum* (Molluginaceae) and *Stegnosperma* (Phytolaccaceae); and crystalloid-free, having only the ring, found in two families, the Amaranthaceae and the Chenopodiaceae.

In an effort to assess the degree of relationship between the anthocyanin families, Caryophyllaceae and Molluginaceae, to the betalain families, and to clarify the disputed relationships of four small families, Achatocarpaceae, Batidaceae, Gyrostemonaceae, Theligonaceae, to the Centrospermae, the pollen of 190 species from 16 families was examined (Nowicke, 1975). The significant result with the attendant conclusion was: the vast majority of the taxa examined in the betalain families, as well as the two anthocyanin families, Caryophyllaceae and Molluginaceae, had pollen grains with a very similar, sometimes indistinguishable morphology; and the two groups are very closely related to each other. Approximately 85% of the species examined had a tectum which could be described as spinulose and/or perforate, punctate, or tubuliferous. The pollen morphology of each of the four small families mentioned above does not support a relationship to the Centrospermae, nor to any of the remaining three for Achatocarpaceae or for Theligonaceae. The Batidaceae and Gyrostemonaceae have in common several unusual features, including the structure of the exine, and will be discussed in this paper.

The structure of the exine in the centrospermous families was the subject of a paper by Skvarla & Nowicke (1976), in which 33 genera from 11 families were examined in thin section. All 33 taxa had an exine organized into the foot layer, columellae, and tectum units considered typical for the angiosperms. With a few exceptions the endexine is poorly developed, sometimes apparently absent. Any noteworthy characteristics found in thin section in the 1976 study or in subsequent ones will be discussed under the particular family.

Sixteen families, Phytolaccaceae, Nyctaginaceae, Portulacaceae, Amaranthaceae, Chenopodiaceae (including Dysphaniaceae), Caryophyllaceae, Cactaceae, Aizoaceae, Molluginaceae, Basellaceae, Didiereaceae, Halophytaceae, Achatocarpaceae, Theligonaceae, Gyrostemonaceae, and Batidaceae will be discussed according to phylogenetic relationships where feasible; changes or implications brought out by subsequent investigations (Skvarla & Nowicke, 1976; Nowicke & Skvarla, 1977, 1979, etc.) will be included with the particular family.

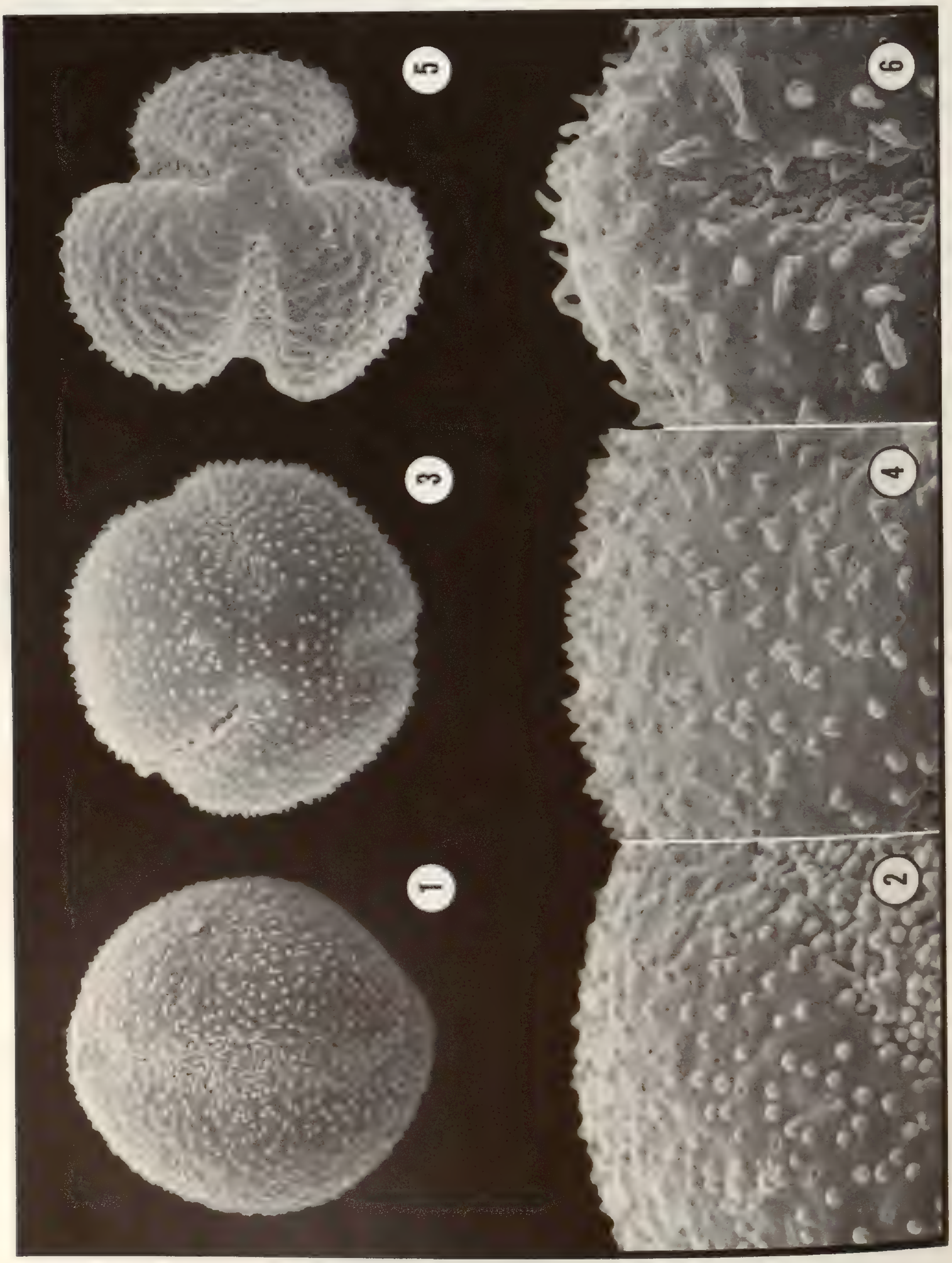
PHYTOLACCACEAE

The modern concept of the Phytolaccaceae includes 17 genera and perhaps as many as 80 species, distributed mostly in the warmer regions of the New World. The family has been considered as the most primitive in the order, and Buxbaum (1961) has referred to *Phytolacca* as the primordial genus, noting the similarity of the free carpelled species (sect. *Pircunia*, e.g., *P. acinosa*) to *Pereskia* (Cactaceae) and *Illicium*, a monotypic family in the Magnoliales. It might be more accurate to describe the family as unspecialized in view of the random variation in the floral parts: a calyx of four or five segments, usually dry and inconspicuous; the corolla absent; the stamens vary in number and placement within species, plants or even inflorescences; the position of the ovary, the carpel number, and the extent to which they are united can also vary within a species and within an inflorescence.

The pollen morphology has been thoroughly investigated by Bortenschlager (1973) and by Nowicke (1968). All taxa have the spinulose and punctate/perforate tectum and apertures that are 3-colpate, pantoporate, or pantocolpate. The six taxa illustrated in SEM by Nowicke (1975: figs. 1–6) are representative of the Phytolaccaceae. In this paper *Phytolacca americana* and *Stegnosperma halimifolium* are illustrated in SEM and in TEM, Figs. 15 and 46, and 18 and 47, respectively. The unspecialized exomorphology is reflected in the structure of the exine: Fig. 46, a section through the mesocolpus of *Phytolacca americana*, and Fig. 47, a section of a whole grain of *Stegnosperma halimifolium*, have the foot layer, columellae and tectum represented in a manner typical of the dicots. An accumulation of endexine in the region of the aperture is a common characteristic in the Phytolaccaceae (Fig. 47), the Centrospermae, and dicots in general. But, for the most part, the Centrospermae do not have a well-developed endexine in nonapertural regions; in Fig. 46, it is represented by the slightly less electron dense "layer" most evident at the far right. *Microtea paniculata* has pollen which is pantoporate (Nowicke, 1975: fig. 4) and in thin section (Skvarla & Nowicke, 1976: fig. 37) the thicker tectum and thinner foot layer are more similar to some Caryophyllaceae (Skvarla & Nowicke, 1976: fig. 46, *Dianthus barbatus*; Nowicke & Skvarla, 1977: fig. 23, *Gymnocarpos fruticosum*) than to any phytolaccaceous taxa sectioned thus far.

NYCTAGINACEAE

The Nyctaginaceae with 28–30 genera and perhaps 250 species is found mostly in the tropics and subtropics of the New World. This family has the widest range of variation in pollen morphology and the different types fall along tribal and subtribal lines as established by Heimerl in 1934. In earlier contributions, Now-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icke (1970: figs. 1–18), Nowicke & Luikart (1971: figs. 1–14, 16–19), Nowicke (1975: figs. 7–12, 78–79, 82, 85), Skvarla & Nowicke (1976: figs. 10, 30–34), and Nowicke & Skvarla (1977: figs. 18, 27), illustrated the different types in SEM and TEM.

The subtribe Mirabileae has pollen characterized by very large, spherical grains, ca. 100–180 μm in diameter, numerous small pores, very thick walls, and a spinulose and tubuliferous and/or perforate tectum (at least some tubules appear to be collapsed spines). *Boerhaavia erecta*, Fig. 7–8, and 40, is representative of this group (see also Nowicke, 1975: figs. 12, 78). The greatly enhanced foot layer, Fig. 40, accounts for much of the thickness of the exine.

The subtribe Abroniinae with only *Abronia* (Nowicke & Skvarla, 1977: figs. 18, 27) and the subtribe Bougainvilleinae with only *Bougainvillea* (Nowicke, 1975: fig. 11; Skvarla & Nowicke, 1976: fig. 33) have 3(–4)-colpate grains with an incomplete tectum of a reticulate configuration with numerous free columellae in the lumina.

The subtribe Phaeoptilinae with only *Phaeoptilum* (Nowicke, 1975: fig. 10) has pantocolpate (4-4-4) grains with a spinulose and punctate tectum.

The tribe Colignonieae with only *Colignonia* (Nowicke & Luikart, 1971: figs. 1–4) has pantoporate grains with a spinulose and perforate tectum. But the pores are fewer and larger than in the subtribe Mirabileae and can be arranged 4-4-4, rarely 5-5-5; the spines not nearly so prominent.

The tribe Boldoeae (Nowicke & Luikart, 1971: figs. 5–10) has three genera, *Boldoa*, *Cryptocarpus* (Nowicke, 1975: fig. 7) and *Salpianthus*, illustrated here by *S. arenarius*, Figs. 14, 44, all of which are 3-colpate with a spinulose and perforate tectum.

The TEM of *Salpianthus*, Fig. 44, is noteworthy for the following reasons: the foot layer is unusually thick and not an artifact since the presence of at least some continuous columellae indicates that the angle of section is only slightly oblique; the tectum is perforate and well developed; lastly, there is a thin, uniform endexine.

The tribe Leucastereae (Nowicke & Luikart, 1971: figs. 13–14, 16–19) has four genera, three of which, *Andradea* (fig. 17), *Leucaster* (fig. 16), and *Ramisia* (fig. 18) have 3-colpate grains with a spinulose and punctate tectum. *Reichenbachia hirsuta*, Figs. 20, 56, however, has an incomplete tectum of a reticulate configuration. The lumina are smaller than those found in *Abronia* and *Bougainvillea* and lack any free columellae. The most notable feature in thin section is the lamellar nature of the endexine.

The tribe Pisonieae has at least six genera, *Calpidia*, *Cephalotomandra*, *Neea*, *Pisonia*, *Pisoniella*, *Rockia*, that have 3-colpate, 6-pantocolpate, 12- or 15-pantocolpate (arranged 4-4-4, 5-5-5), rarely 18-pantocolpate (6-6-6) grains. More than one aperture type can be found in a species or in a sample. With the exception

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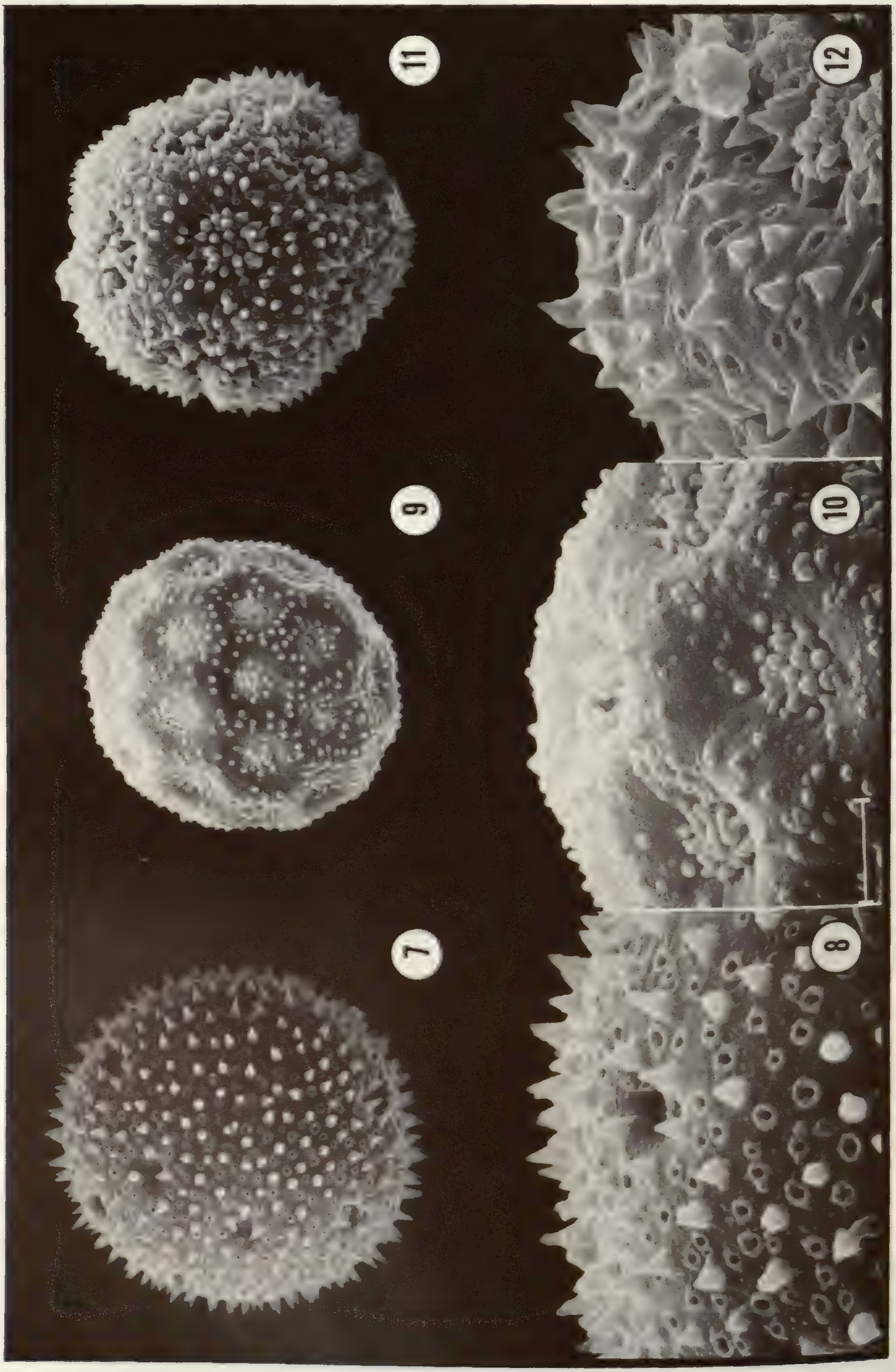
FIGURES 1–6. Scanning Electron Micrographs of Centrospermae pollen.—1. *Gisekia pharnaceoides* L. (Aizoaceae), equatorial view, ×3,000.—2. *G. pharnaceoides*, ektexine surface, ×7,900.—3. *Tetragonia vestita* I. M. Johnston (Aizoaceae), polar view, ×1,900.—4. *T. vestita*, ektexine surface, ×5,900.—5. *Ceraria fruticulosa* Pears. & Steph. (Portulacaceae), polar view, ×1,900.—6. *C. fruticulosa*, ektexine surface, ×5,900.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of *Neea* (Nowicke, 1975: fig. 9), all taxa examined have a spinulose and punctate/perforate tectum (Nowicke, 1975: fig. 79). Some species of *Neea* have an incomplete tectum of a reticulate configuration but with smaller lumina than in *Abronia*, *Bougainvillea*, or *Reichenbachia*. The only member of this tribe examined in thin section is *Pisonia aculeata* (Skvarla & Nowicke, 1976: fig. 31). Some of the irregularity of the foot layer, stalactite-stalagmite appearance of the columellae, and thickened tectum are an artifact of the oblique angle of section.

PORTULACACEAE

For the Portulacaceae, a betalain family with as many as 350 species segregated into 19 genera, additional sampling has not revealed any unusual morphologies. Twenty-two species have been examined in these studies (Nowicke, 1975; Skvarla & Nowicke, 1976; Nowicke & Skvarla, 1977), one of which, *Montia meridensis*, is illustrated in SEM for the first time in Fig. 19. The grain is 15-pantocolpate, the colpi arranged in a 5-5-5 pattern, and has an incomplete tectum which could also be described as finely reticulate. A paucity of material prevented examination in TEM or confirmation of the above, but there is no apparent reason to question the results. The pollen morphology of *Montiastrum* (Nowicke, 1975: fig. 18) is highly specialized and these grains could be distinguished from all other taxa examined in the Centrospermae and those in subsequent studies.

Twenty of the 22 species examined in the Portulacaceae have the spinulose and punctate/perforate tectum, differing mostly in the type of aperture: 3-colpate includes *Ceraria fruticulosa*, Figs. 5–6, and *Lenzia chamaepitys*, Fig. 13; pantocolpate includes *Talinum paniculatum* (Nowicke, 1975: fig. 16), *Portulaca grandiflora* (Nowicke, 1975: fig. 17), and *Naiocrene parvifolia* (Nowicke & Skvarla, 1977: figs. 6, 10, 28); pantoporate includes *Calandrinia ciliata* and *C. sericea* (Nowicke, 1975: fig. 15). The pollen of the last two species is very similar to some in the Cactaceae (Nowicke, 1975: figs. 19–20), Caryophyllaceae, Figs. 25, 31, and Chenopodiaceae, Figs. 28, 34: all have pores which are large in size, reduced in number, and symmetrically placed.

In TEM the exine of the Portulacaceae has a wider range of variation than most of the centrospermous families. Figure 39, *Ceraria fruticulosa*, illustrates a fragmented endexine, an irregular foot layer, variable columellae, and a well-developed tectum. At least part of the irregularity is the result of the slightly oblique angle of the section.

The exine structure of *Portulacaria afra* (Skvarla & Nowicke, 1976: fig. 39) is very similar to that of *Ceraria fruticulosa*, Fig. 39. *Calyptridium umbellatum* (Skvarla & Nowicke, 1976: fig. 38) and *Naiocrene parvifolia* (Nowicke & Skvarla, 1977: fig. 28) have a uniform foot layer, columellae which are regular in shape and distribution, and a tectum which is consistent with that depicted in SEM (Nowicke, 1975: fig. 14; Nowicke & Skvarla, 1977: figs. 6, 10). The exine of

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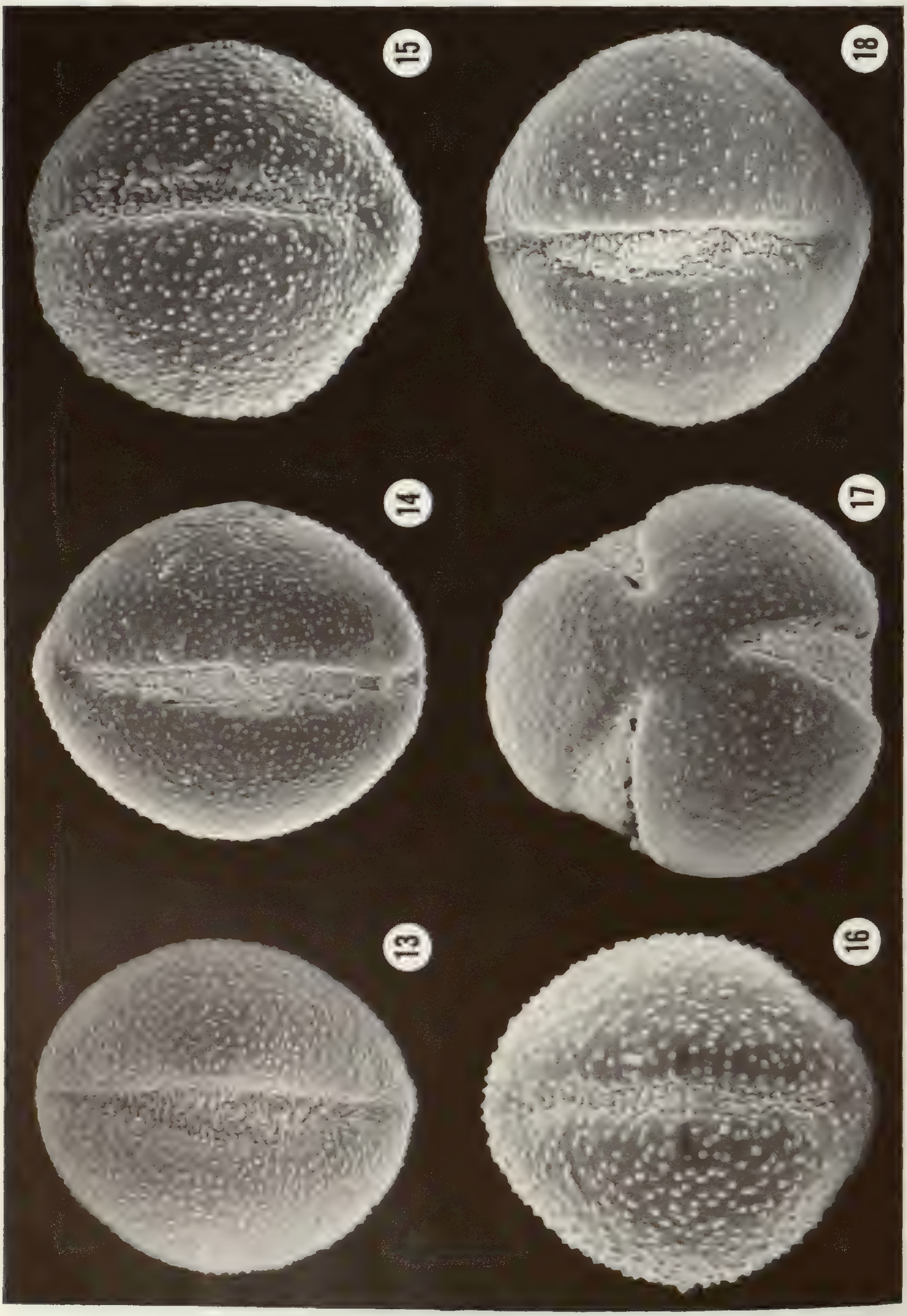
FIGURES 7–12. Scanning Electron Micrographs of Centrospermae pollen.—7. *Boerhaavia erecta* L. (Nyctaginaceae), ×890.—8. *B. erecta*, ektexine surface, ×2,300.—9. *Beta vulgaris* L. (Chenopodiaceae), ×2,980.—10. *B. vulgaris*, ektexine surface, ×7,700.—11. *Alluaudia humbertii* Choux (Didiereaceae), ×920.—12. *A. humbertii*, ektexine surface, ×3,850.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Portulaca grandiflora (Skvarla & Nowicke, 1976: fig. 40) is distinguished by the very thin foot layer, short, thick and sparsely distributed columellae supporting a thin tectum with prominent spines (Nowicke, 1975: fig. 81).

Unfortunately, the number of species examined in the Portulacaceae is insufficient to test McNeill's (1974) revised classification, but at this time it seems unlikely that pollen morphology will be a critical or key characteristic at any level. McNeill's (p. 726) first couplet for the key to tribes includes "pollen poly (30)-pantocolpate" versus "pollen various, very rarely polypantocolpate." At that time the pantocolpate characteristic was applicable only to *Portulaca*. But pollen studies since 1974 have reported this condition in species identified as belonging to *Anacampseros* (unpublished data), *Montia meridensis*, Fig. 19, *Naiocrene* (Nowicke & Skvarla, 1977: fig. 10), and *Talinum* (Nowicke, 1975: fig. 16). The apparent lack of agreement does not necessarily question McNeill's concept of the infrafamilial classification, but may indicate that the palynological data have limited value at that level. All available evidence from pollen morphology does confirm the close relationship of the Portulacaceae to the betalain families and the Caryophyllaceae and Molluginaceae.

AMARANTHACEAE AND CHENOPODIACEAE

The Amaranthaceae and Chenopodiaceae have long been considered as closely related families: congested inflorescences with small, reduced flowers, the unilocular, 2–3-carpelled ovary, etc. The Chenopodiaceae is the larger family, with about 100 genera and 1,400 species, many with adaptations for physiologically dry habitats in temperate regions; the Amaranthaceae, with 64 genera and 800 species, is most abundant in tropical and subtropical regions.

Their close affinity to each other is reinforced by the peculiar variant of the protein of the sieve-tube plastid, which has only the peripheral ring of fibrous protein (Behnke, 1976: figs. 10, 12c, 13). The central crystalloid protein, found in all remaining betalain families and the Caryophyllaceae and Molluginaceae, is absent. The pollen morphology of the Chenopodiaceae and Amaranthaceae is also unusual: all taxa have grains which are pantoporate (Nowicke, 1975; Skvarla & Nowicke, 1976; Nowicke & Skvarla, 1977). It is the negative aspect of this distribution that is perplexing: the absence of the basic 3-colpate type, especially in a family as large as Chenopodiaceae, could indicate that the ancestral branch which gave rise to these two families was, at that time, a constricted one.

The Amaranthaceae and the Chenopodiaceae have the spinulose and punctate tectum but the perforations are very small and sparsely distributed, and in fact best illustrated in thin section, Figs. 41–42, 48, 52 (Skvarla & Nowicke, 1976: figs. 14, 23–27; Nowicke & Skvarla, 1977: figs. 20, 25), as opposed to SEM, Figs. 9–10, 28–30, and 34–36.

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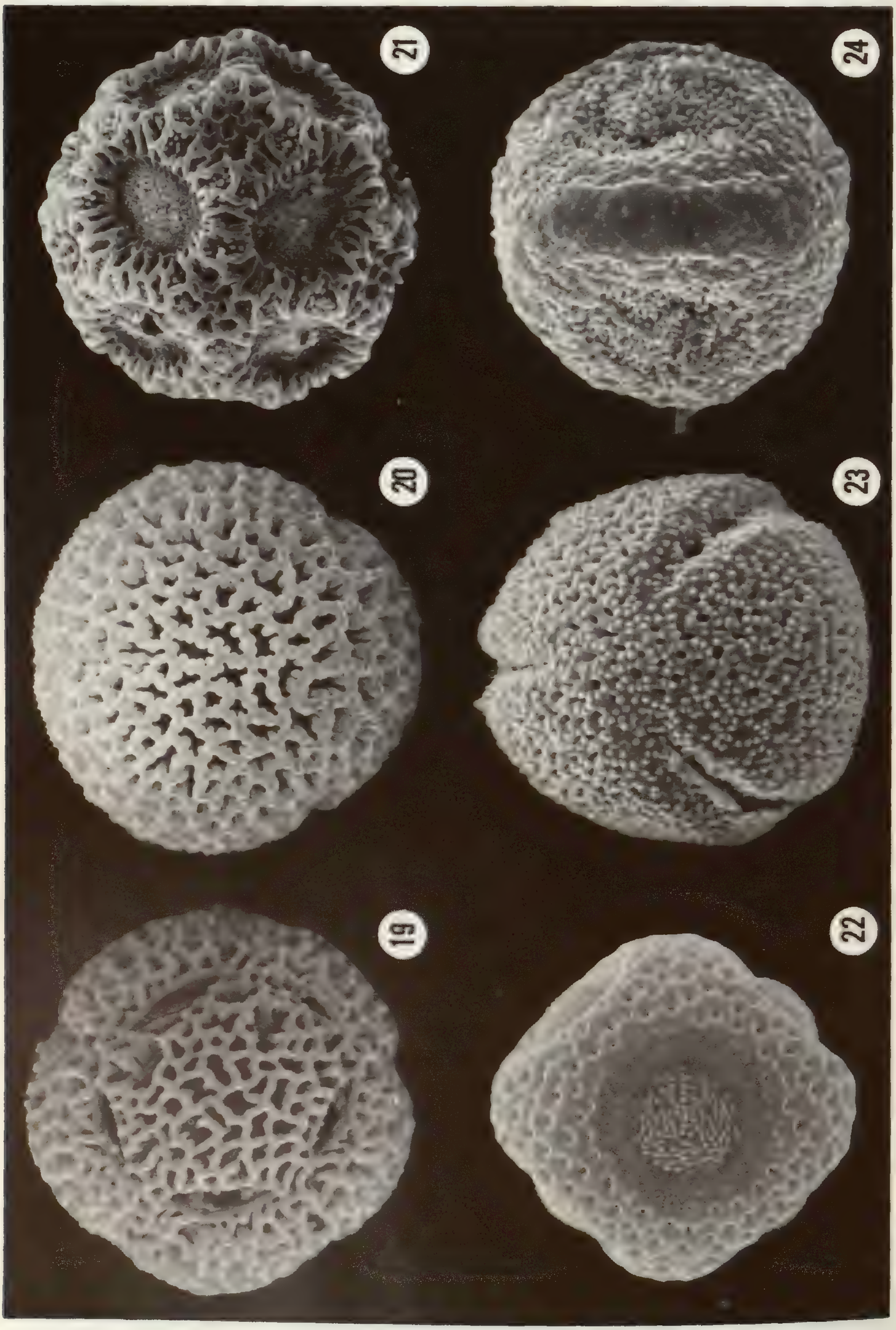
FIGURES 13–18. Scanning Electron Micrographs of Centrospermae pollen.—13. *Lenzia chamaepitys* Phil. (Portulacaceae), equatorial view, ×1,620.—14. *Salpianthus arenarius* H. & B. (Nyctaginaceae), equatorial view, ×1,930.—15. *Phytolacca americana* L. (Phytolaccaceae), equatorial view, ×2,430.—16. *Pharnaceum incanum* L. (Aizoaceae), equatorial view, ×3,230.—17. *Cometes surattensis* L. (Caryophyllaceae), polar view, ×1,850.—18. *Stegnosperma halimifolium* Benth. (Phytolaccaceae), equatorial view, ×1,770.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The Amaranthaceae is divided into two subfamilies, Amaranthoideae and Gomphrenoideae, based on anther locules, 4 versus 2, respectively, and the ovary with one to many ovules versus always one ovule.

Within the taxa examined, the pollen of the Amaranthoideae can have pores which are small, numerous, not sunken, e.g., *Amaranthus* (Nowicke, 1975: fig. 56); or, larger and fewer pores, slightly recessed, e.g., *Aerva* (Nowicke, 1975: fig. 58), *Marcelliopsis* (Nowicke, 1975: fig. 57).

An unusual characteristic is found in some taxa in the Amaranthoideae: aperture plates that have four, five, or six identically shaped, recurved spines that produce a starlike structure. This condition is illustrated in *Pupalia lappacea* (Nowicke, 1975: fig. 59), and *Psilotrichum amplum* (Nowicke & Skvarla, 1977: figs. 13, 20). It is also present to varying degrees in *Aerva* (Townsend, 1974), *Centemopsis,* and *Robynsiella* (Livingstone et al., 1973).

The pollen in the subfamily Gomphrenoideae can be distinguished from that found in the Amaranthoideae or in the Chenopodiaceae by pores which are recessed, are separated by one, rarely two rows of columellae, and are either large and few in number, or small and more numerous. In each case apertures cover the surface of the grain. Those taxa with large pores include: *Alternanthera flavescens,* Fig. 36, *Gomphrena elegans,* Fig. 29, *Iresine angustifolia,* Fig. 30, *Pfaffia iresinoides,* Fig. 35, and *Tidestromia lanuginosa* (Nowicke, 1975: fig. 52). In *Brayulinea* (Nowicke, 1975: fig. 50) and particularly *Froelichia* (Skvarla & Nowicke, 1976: figs. 6, 10) the pores are smaller and more numerous. Whether each of the pores depicted in those taxa could function in germination is questionable, as is the adaptive value of numerous pores, or the selective pressures which could be responsible.

Thin section verifies the minimal separation of the pores in the Gomphrena types: Fig. 49, *Gomphrena elegans,* is a radial section parallel to the long axis of one murus (left), through the pore, slightly oblique to the long axis of the next murus. In an earlier study (Skvarla & Nowicke, 1976: figs. 16–18) the structure of the exine in *Gomphrena elegans* was clarified by three separate thin sections: parallel with a murus (fig. 16), through a sunken aperture in which the membrane is covered with flecks of ektexine (fig. 18), and a tangential section (fig. 17) illustrating the uniseriate row of columellae separating adjacent pores. The TEMs of *Iresine angustifolia,* a slightly oblique section through the murus in Fig. 52, and through the aperture in Fig. 53, agree with the surface morphology illustrated in SEM, Fig. 30.

The Chenopodiaceae, although a much larger family than Amaranthaceae, does not have a counterpart to the Gomphrena type. It does have taxa whose pollen closely resembles that of *Amaranthus,* i.e., numerous small pores, e.g.,

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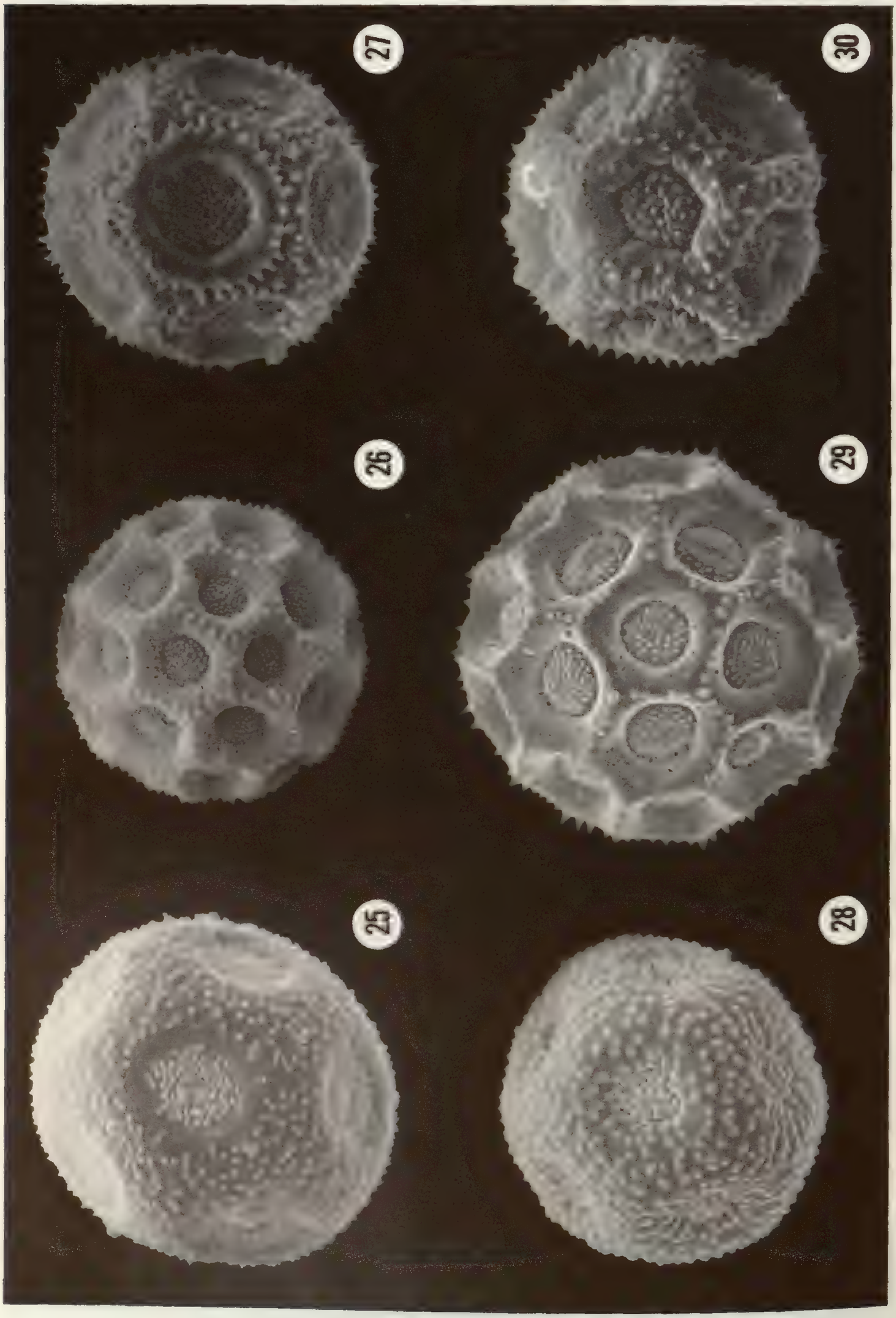
FIGURES 19–24. Scanning Electron Micrographs of Centrospermae pollen.—19. *Montia meridensis* Friedr. (Portulacaceae), polar view, pantocolpate, ×1,480.—20. *Reichenbachia hirsuta* Spreng. (Nyctaginaceae), oblique polar view, 3-colpate, ×2,740.—21. *Opuntia lindheimeri* Engelm. (Cactaceae), ×640.—22. *Basella excavata* S. Ell. (Basellaceae), ×2,740.—23. *Delosperma ecklonis* Schwantes (Aizoaceae), oblique polar view, ×4,030.—24. *Herniaria glabra* L. (Caryophyllaceae), equatorial view with prominent mesocolpial ridge, ×4,180.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Beta vulgaris, Figs. 9–10, *Chenopodium* (Nowicke & Skvarla, 1977: figs. 5, 25), *Grayia* (Nowicke, 1975: fig. 43), and *Borsczowia* (Nowicke, 1975: fig. 45).

A second pollen morphology found in *Anabasis setifera*, Fig. 28, *Halocharis* (unpublished data), *Nitrophila occidentalis*, Fig. 34, and *Traganum* (Nowicke, 1975: fig. 46), is distinguished by fewer, larger, slightly sunken pores, characteristics which, in combination, produce a polyhedrallike shape. Although similar to *Aerva* and *Marcelliopsis* (see above discussion) of the Amaranthaceae, the closest counterparts of these chenopodiaceous taxa are in the Caryophyllaceae: *Cerastium* (Nowicke, 1975: fig. 32), *Paronychia fastigiata*, Fig. 31, *P. canadensis* (unpublished data), *Sclerocephalus arabicus*, Fig. 25, *Scleranthus perennis* (Nowicke, 1975: fig. 31), and *Gymnocarpos* (Nowicke & Skvarla, 1977: fig. 4).

The Chenopodiaceae have an exine structure that could be characterized by Fig. 48, a radial section of *Anabasis setifera*: a thick, sparsely perforate tectum supported by prominent columellae which rest on a relatively thin foot layer (see also Skvarla & Nowicke, 1976: figs. 22–27). Within the Centrospermae this family had the most consistent presence of endexine (Skvarla & Nowicke, 1976: figs. 26–27). Figure 41 of *Beta vulgaris* is a section parallel with the mesoporal ridge; Fig. 42 is a radial section that cuts across two pores and at a right angle to the mesoporal ridge, illustrating the convex structure. The type of pollen morphology found in *Dysphania* (Nowicke, 1975: fig. 60) would support its inclusion in the Chenopodiaceae, as would the plastid subtype (Behnke & Turner, 1971) which lacks the central crystalloid.

CARYOPHYLLACEAE

The systematic significance of the pollen morphology of the Caryophyllaceae was the thrust of the original investigation, "Pollen Morphology in the Order Centrospermae" (Nowicke, 1975), and the irrefutable conclusion, documented by an extensive series of SEM micrographs (Nowicke, 1975: figs. 25–36, 74, 76, 84, 86, 88–89), was that, palynologically, the Caryophyllaceae are very closely related to the betalain families. Twenty-eight of the 33 species examined in that study had the spinulose and punctate/perforate tectum, 25 of the 33 were pantoporate, the remaining 8 were 3-colpate. Four collections variously identified as belonging to *Lychnis* (Nowicke, 1975: figs. 35–36, 84, 88), *Silene* (Nowicke, 1975: figs. 29–30, 89), or *Melandrium* (Skvarla & Nowicke, 1976: figs. 5, 12, 45) had a tectum in which the perforations were sufficiently large to be described as "reticulate," but the decision was and is an arbitrary one. Pantocolpate forms have been reported by other workers (Erdtman, 1966; Vishnu-Mittre & Gupta, 1964), but this condition has not been found in any of the species examined since the first study.

Figures 13 through 18 illustrate the similarity of the 3-colpate, spinulose/punc-

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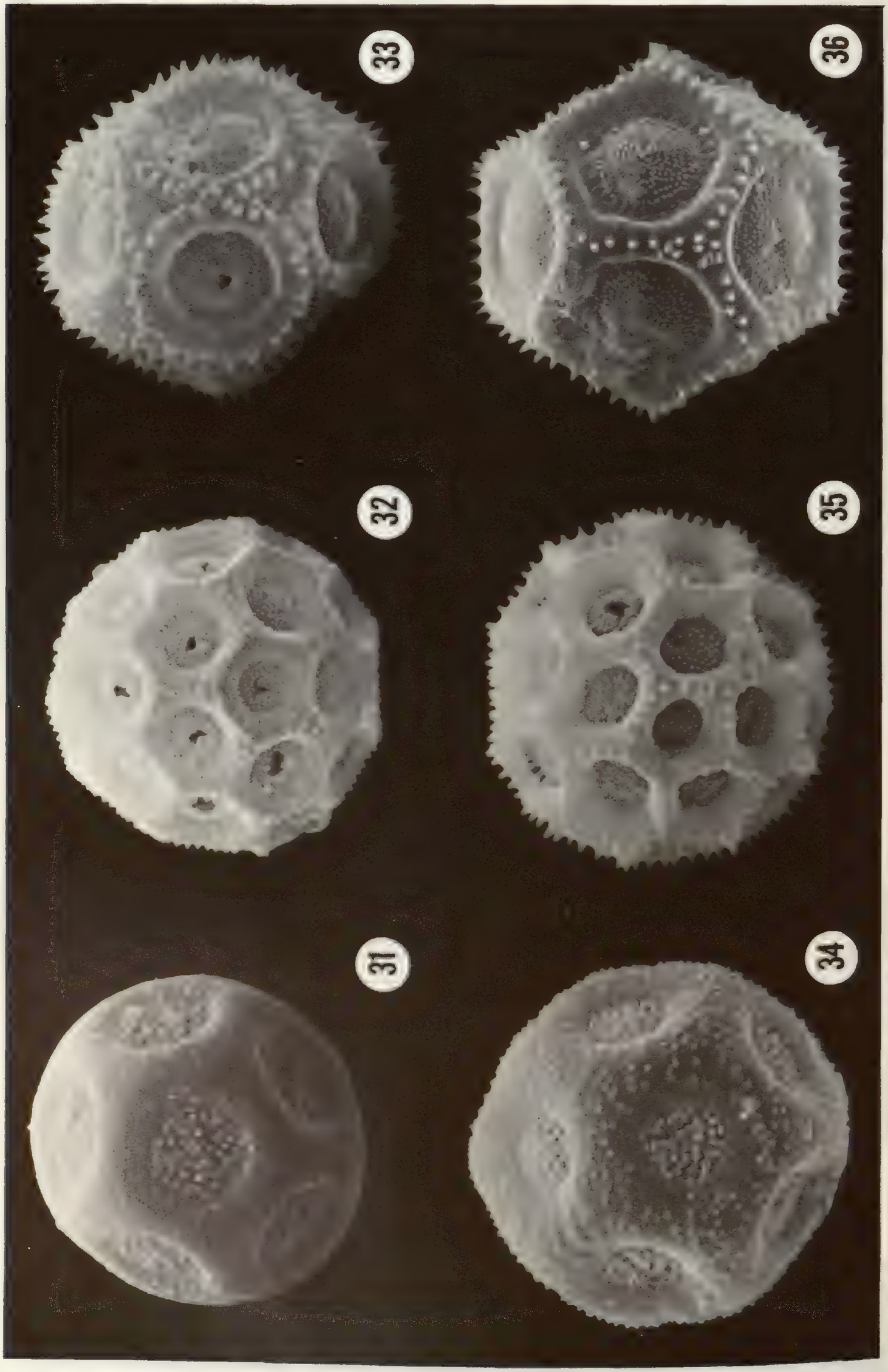
FIGURES 25–30. Scanning Electron Micrographs of Amaranthaceae, Caryophyllaceae, and Chenopodiaceae pollen.—25. *Sclerocephalus arabicus* Boiss. (Caryophyllaceae), ×2,810.—26. *Siphonychia diffusa* Chapm. (Caryophyllaceae), ×3,190.—27. *S. americana* (Nutt.) T. & G., ×3,310.—28. *Anabasis setifera* Moq. (Chenopodiaceae), ×4,100.—29. *Gomphrena elegans* Mart. (Amaranthaceae), ×3,900.—30. *Iresine angustifolia* Euphr. (Amaranthaceae), ×3,750.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tate pollen type in the Centrospermae, and as such confirm the close relationship of the families represented: Fig. 13, *Lenzia chamaepitys*, Fig. 14, *Salpianthus arenarius*, Fig. 15, *Phytolacca americana*, Fig. 16, *Pharnaceum incanum*, Fig. 17, *Cometes surattensis*, and Fig. 18, *Stegnosperma halimifolium*.

The structure of the exine in thin section, e.g., *Cometes surattensis*, Fig. 45, and *Corrigiola* (Skvarla & Nowicke, 1976: fig. 42) closely resembles that of the betalain families, e.g., Fig. 44, *Salpianthus arenarius*, Fig. 46, *Phytolacca americana*, Fig. 47, *Stegnosperma halimifolium*, and Fig. 54, *Basella excavata*.

Figure 24, a whole grain, equatorial view of *Herniaria glabra*, is unusual in the presence of three large, poorly defined aperture areas, separated by a prominent mesocolpial ridge. There is a resemblance to the *Polygonum convolvulus* morphology in Fig. 103. However, the *P. convolvulus* type represents a complex morphology in which the two types of surface tectum are sharply demarcated from each other, and there is a zonorate endoaperture which is conspicuous in LM due to the thickened margins. Thin section of *H. glabra*, Fig. 58, illustrates an aperture with part of the mesocolpial ridge on each side. This structural organization contrasts sharply with the section of *P. convolvulus*, Fig. 109, in which, among other differences, the two apertures are underlain by a prominent endexine. This morphology is a fairly common one in the Polygonaceae and includes those taxa usually assigned to the genus *Polygonella* as well. *Illecebrum verticillatum* is the only other species in the Caryophyllaceae with a morphology similar to that in Fig. 24. *Herniaria hemistemon* and *H. hirsuta* (unpublished data) have pantoporate, spherical grains.

There have been any number of perplexing and unexpected results in these pollen studies: the structure of the exine in Batidaceae and Gyrostemonaceae; the magnitude of the distinction between the Armeria type and the Plumbago type in the Plumbaginaceae (Nowicke & Skvarla, 1977); the compacted columellae found in the *Bistorta* complex of *Polygonum* (Nowicke & Skvarla, 1977); and the close similarity in SEM of the Ranunculaceae and Centrospermae pollen are but a few. The most recent of these concerns the relationships of the Caryophyllaceae.

The placement of the Caryophyllaceae in the dicot hierarchy seems to reflect the nature of the latest discovery. Classical morphology allied the family with the Centrospermae. The presence of the anthocyanins as opposed to betacyanins seemed to dismiss the possibility of including the family in the Centrospermae (an opinion formerly held by the first author). Behnke's work on sieve-tube plastids (Behnke, 1976), the presence of a very distinctive type found only in the betalain families *and* Caryophyllaceae and Molluginaceae as well, created doubt, the more so the larger his sample size became. Neither author would be so presumptuous as to regard the recent results in the Caryophyllaceae as being

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FIGURES 31–36. Scanning Electron Micrographs of Amaranthaceae, Caryophyllaceae, and Chenopodiaceae pollen.—31. *Paronychia fastigiata* (Raf.) Fern. (Caryophyllaceae), ×3,260.—32. *Siphonychia rugelii* Chapm. (Caryophyllaceae), ×2,820.—33. *S. pauciflora* Small, ×3,330.—34. *Nitrophila occidentalis* S. Wats. (Chenopodiaceae), ×2,940.—35. *Pfaffia iresinoides* (H.B.K.) Spreng. (Amaranthaceae), ×3,300.—36. *Alternanthera flavescens* H.B.K. (Amaranthaceae), ×3,550.

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equal in significance to the pigment dichotomy or the plastid similarity, but there is unmistakable evidence of a very close tie between the Caryophyllaceae and the Amaranthaceae.

Siphonychia is a small caryophyllaceous genus of 5 or 6 species distributed along the warmer regions of the Atlantic seaboard. Six collections variously identified as *S. americana*, Fig. 27 (Nowicke & Skvarla, 1977: fig. 14), *S. diffusa* Fig. 26, *S. erecta*, *S. pauciflora*, Fig. 33, and *S. rugelii*, Fig. 32, were examined in LM and SEM; *S. americana* was also examined in TEM, Figs. 50 and 51. Two distinctive, yet related pollen types were found. The first type consists of grains with small (relative to the other type) pores, ca. 20 to 24(?) in number, deeply (relative to the other type) sunken, each pore separated from the adjacent ones by a single(?) row of columellae with a "tectum" that extends down their sides. Examples of this type include: *S. diffusa*, Fig. 26, *S. erecta*, and *S. rugelii*, Fig. 32. The close similarity of these specialized grains to those found in the amaranthaceous taxa, *Gomphrena elegans*, Fig. 29, and *Pfaffia iresinoides*, Fig. 35, is remarkable. The second pollen type, found in *S. americana*, Fig. 27, and *S. pauciflora*, Fig. 33, is characterized by larger pores, fewer in number, with each delimited by a ringlike border having a fringe of small spines. *Alternanthera flavescens*, Fig. 36, from the Amaranthaceae, is almost indistinguishable from *S. americana* and *S. pauciflora*. Other closely related taxa include *Iresine angustifolia*, Fig. 30, *Tidestromia lanuginosa* (Nowicke, 1975: fig. 52), and *T. oblongifolia* (unpublished data). The thin sections of *S. americana*, Figs. 50 and 51, reveal a reduction of mesoporous exine similar to that in *Gomphrena elegans*, Fig. 49, and in *Iresine angustifolia*, Figs. 52 and 53.

To regard this type of similarity, a highly specialized pollen morphology not found elsewhere in the Centrospermae, in any of the other families examined in these studies, or in the literature (to the best of our knowledge), as parallelism is absurd.

Few taxonomists would dispute the close relationship of the Amaranthaceae and Chenopodiaceae, frequently cited as an example of "twin families." Yet the results from this palynological investigation suggest that the Amaranthaceae and Chenopodiaceae are more closely related to certain separate groups in the Caryophyllaceae than they are to each other. Surely the *Siphonychia-Alternanthera*, *Gomphrena*, *Pfaffia*, *Iresine* bond is more substantial than that of *Amaranthus-Chenopodium*. And, while the pollen morphology found in *Anabasis setifera*, Fig. 28, *Halocharis* spp. (unpublished data), *Nitrophila occidentalis*, Fig. 34, and *Traganum* (Nowicke, 1975: fig. 46) is less specialized than either the Gomphrena or Siphonychia types, the closest counterparts are found in the caryophyllaceous genera, *Cerastium* (Nowicke, 1975: fig. 32), *Drypis* (Nowicke, 1975: fig. 34), *Gymnocarpos* (Nowicke & Skvarla, 1977: fig. 4), *Paronychia fastigiata*, Fig. 31,

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FIGURES 37–43. Transmission Electron Micrographs of Centrospermae pollen.—37. *Gisekia pharnaceoides* L. (Aizoaceae), ×6,480.—38. *Tetragonia vestita* I. M. Johnston (Aizoaceae), ×3,600.—39. *Ceraria fruticulosa* Pears. & Steph. (Portulacaceae), ×13,680.—40. *Boerhaavia erecta* L. (Nyctaginaceae), ×4,340.—41. *Beta vulgaris* L. (Chenopodiaceae), ×10,080.—42. *B. vulgaris*, ×10,080.—43. *Alluaudia humbertii* Choux (Didiereaceae), ×3,800.

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Sclerocephalus arabicus, Fig. 25, and *Scleranthus perennis* (Nowicke, 1975: fig. 31), not in the Amaranthaceae.

However, data from all (?) other sources—pigment, plastid subtype, floral morphology—favor the Amaranthaceae-Chenopodiaceae relationship.

CACTACEAE

The Cactaceae was the last major family in which betalains were discovered and its subsequent transfer to the Centrospermae was agreeable to generalists and specialists alike.

This large family, native to the New World, is widely distributed in the arid regions, but is cultivated extensively as ornamentals in the Old World. Generic concepts vary considerably in the Cactaceae, from 50 to as many as 220, and the recognized number of species varies from at least 1,200 to perhaps as high as 2,000. Britton & Rose (1920) described the Cactaceae in a semimonographic treatment in which they recognized approximately 100 genera segregated in three tribes: Pereskieae with only the genus *Pereskia*; Opuntieae with seven genera; and the Cereeae with the remaining and vast majority of genera.

Nowicke (1975) examined the pollen of 12 species. The range of variation illustrated (Nowicke, 1975: figs. 19–24) is, for the most part, representative of the family: the common type of tectum (figs. 19–22), spinulose and punctate/perforate, is distributed across the three aperture types, pantoporate (figs. 19–20), 3-colpate (fig. 21), and pantocolpate (fig. 22). A specialized type in the Cactaceae, polygonal in shape due to the very large, flat apertures which are separated from each other by an incomplete tectum of a reticulate configuration, is illustrated by *Opuntia polycantha* and *O. engelmanni* (Nowicke, 1975: figs. 23–24) in this paper by *Opuntia lindheimeri,* Figs. 21, 57.

In thin section (Skvarla & Nowicke, 1976) *Opuntia fulgida* (fig. 20) and *Echinocercus cinerascens* (fig. 21) have an exine structure consistent with the spinulose, perforate exomorphology.

The structure of the aperture in the Cactaceae is very similar (Skvarla & Nowicke, 1976: fig. 20; Nowicke & Skvarla, 1977: fig. 22) to that in the Didiereaceae, Fig. 43, *Alluaudia humbertii* (see also Skvarla & Nowicke, 1976: fig. 28).

Leuenberger (1976) investigated the pollen of more than 600 species of Cactaceae and produced a classic and definitive study. Many of the important collections of Britton and Rose are deposited at the US National Herbarium and, to the extent possible, Nowicke accommodated Leuenberger's request for pollen samples from critical taxa. However, the holdings at US do not have sufficient depth to permit duplication of efforts and our investigation was terminated. The phrase "readily obtainable" in reference to source material (see Introduction) is

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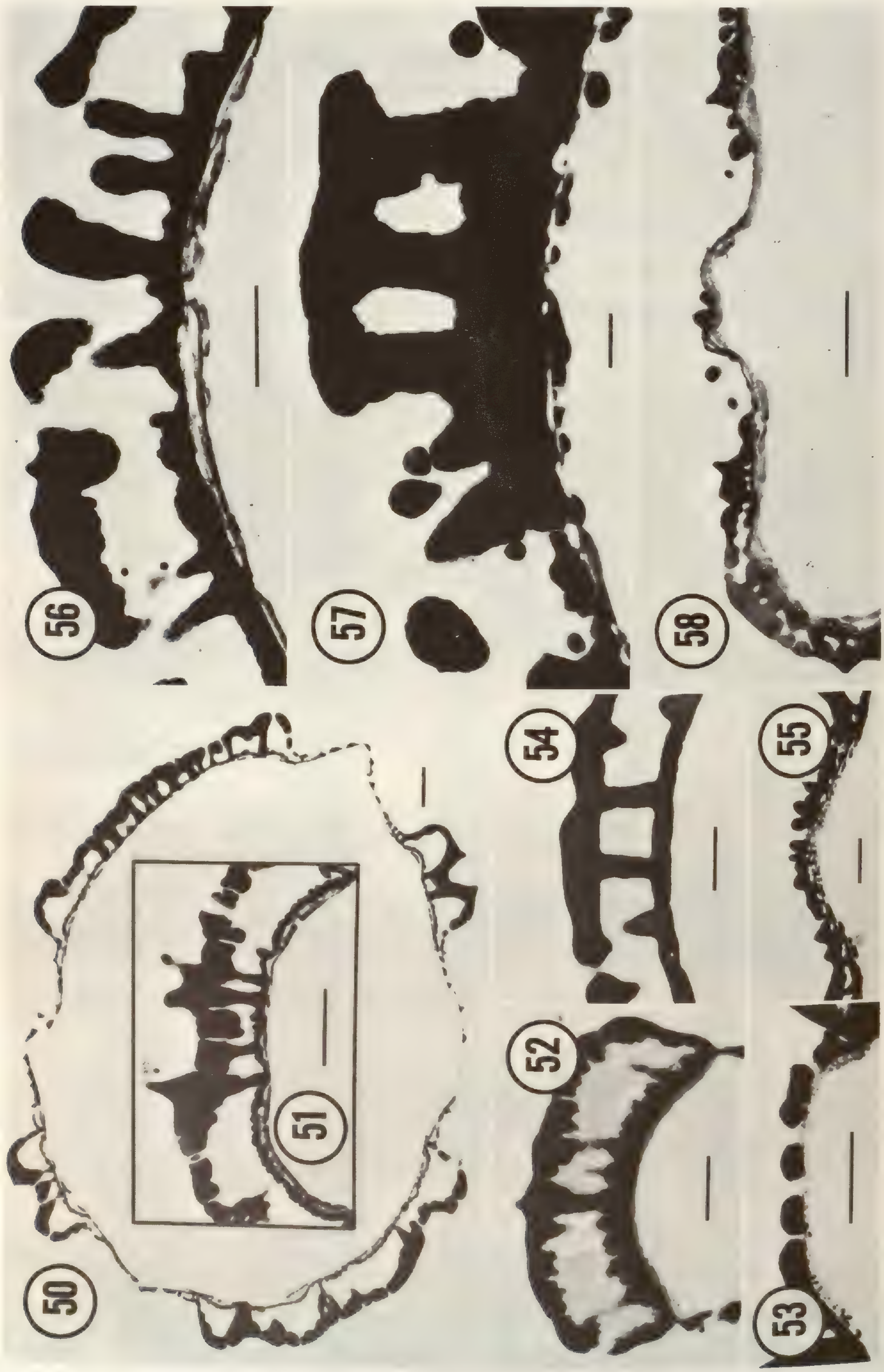
FIGURES 44–49. Transmission Electron Micrographs of Centrospermae pollen.—44. *Salpianthus arenarius* H. & B. (Nyctaginaceae), ×23,220.—45. *Cometes surattensis* L. (Caryophyllaceae), ×16,340.—46. *Phytolacca americana* L. (Phytolaccaceae), ×15,200.—47. *Stegnosperma halimifolium* Benth. (Phytolaccaceae), ×3,000.—48. *Anabasis setifera* Moq. (Chenopodiaceae), ×20,520.—49. *Gomphrena elegans* Mart. (Amaranthaceae), ×8,460.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not to be interpreted as infinite. His report of tetrads in *Pseudorhipsalis himantoclada* (Leuenberger, 1976: 293, plate 13) is not only the first in the family but in the order Centrospermae. Comparison of Leuenberger's (1976, plates 15–18) SEMs of the Cactaceae tectum at high magnification with that of other families in the Centrospermae (Nowicke, 1975: figs. 73–81; Nowicke & Skvarla, 1977: figs. 7–12) should remove any vestige of doubt as to the very close relationship between this family and those remaining in the Centrospermae.

AIZOACEAE AND MOLLUGINACEAE

The definition, the boundaries, and the constituent genera of two families, Aizoaceae and Molluginaceae, vary according to the author, and seemingly no two are in complete agreement. At the one extreme, Pax & Hoffman (1934) relegated the latter to subfamily status under the former, and at the other extreme, some of the larger genera, *Tetragonia, Mesembryanthemum,* etc., are elevated to family status by various authors. The Molluginaceae has been characterized as an anthocyanin family and the Aizoaceae as a betalain family, but the assignment of genera on the basis of the pigment dichotomy applies only to those genera whose pigments have been identified.

Due primarily to lack of material, the pollen morphology in both families was discussed only briefly in the previous publications (Nowicke, 1975; Skvarla & Nowicke, 1976; Nowicke & Skvarla, 1977). The pollen of an additional 15 species representing 9 genera has been examined, Table 1. All taxa from this alliance have the spinulose and punctate/perforate tectum, and with the single exception of *Mollugo verticellata,* which is pantocolpate (Nowicke, 1975: fig. 41), all are 3-colpate.

Species illustrated include: *Gisekia pharnaceoides,* Figs. 1–2, 37; *Tetragonia vestita,* Figs. 3–4, 38; and *Delosperma ecklonis,* Fig. 23. In TEM *Tetragonia,* Fig. 38, has a very thin foot layer in contrast to that found in *Gisekia,* Fig. 37, or in *Mesembryanthemum* (Nowicke & Skvarla, 1977: fig. 19). In Figs. 37 and 38 the endexine is most conspicuous in the aperture regions, but *Mesembryanthemum* (Nowicke & Skvarla, 1977: fig. 19) has a readily defined endexine in what appears to be the mesocolpus.

The pollen of one species of *Acrodon, A. bellidiflorus* (Nowicke & Skvarla, in press), and three of *Delosperma, D. abyssinica, D. ecklonis,* Fig. 23, and *D. mahonii,* was obtained from the herbarium at Kew. Species from these two genera were described as having a reticulate exine by Radulescu (1973). The grain illustrated in Fig. 23 is representative of *Delosperma*; the sample of *Acrodon* contained some grains with slightly larger perforations. Whether the Aizoaceae has pollen with reticulate exines depends on the definition of reticulate. But we would describe the tectum in all four as spinulose and perforate.

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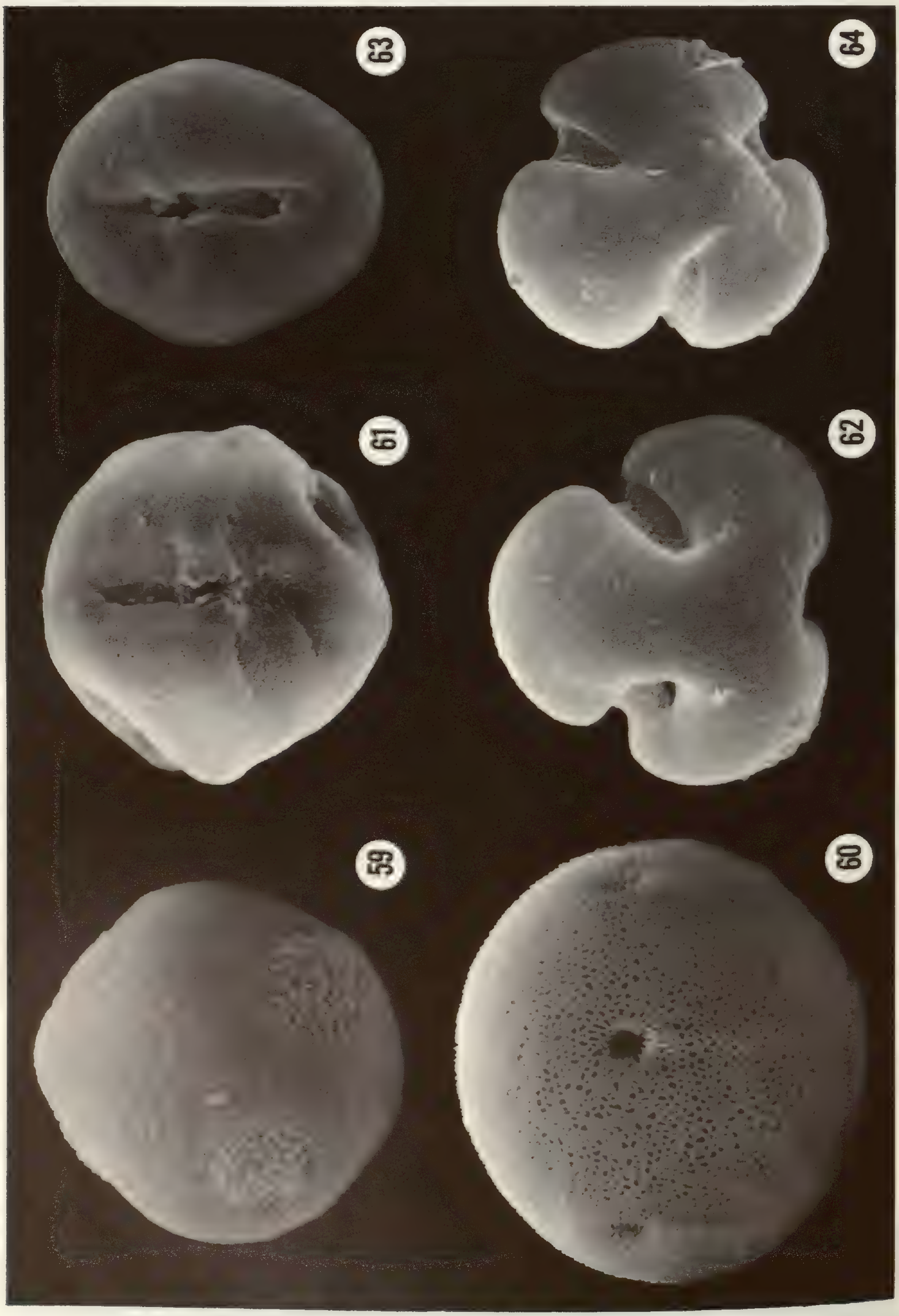
FIGURES 50–58. Transmission Electron Micrographs of Centrospermae pollen.—50. *Siphonychia americana* (Nutt.) T. & G. (Caryophyllaceae), ×5,740.—51. *S. americana,* ×10,260.—52. *Iresine angustifolia* Euphr. (Amaranthaceae), ×8,740.—53. *I. angustifolia,* ×12,600.—54. *Basella excavata* S. Ell. (Basellaceae), ×8,120.—55. *B. excavata,* ×6,670.—56. *Reichenbachia hirsuta* Spreng. (Nyctaginaceae), ×13,630.—57. *Opuntia lindheimeri* Engelm. (Cactaceae), ×7,560.—58. *Herniaria glabra* L. (Caryophyllaceae), ×19,760.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BASELLACEAE

One of the more unusual pollen morphologies in the dicots is found in the small tropical family Basellaceae. Collections identified as *Basella alba* and *B. rubra* have a well-defined cuboidal shape with a colpus on each of the six faces (Nowicke, 1975: figs. 63–65). *Basella excavata*, Fig. 22, has a similar morphology, but the tectum is almost complete (indented punctae), and in thin section, Fig. 54, this species has a readily identified foot layer, columellae, and tectum. A granular endexine is present only in the region of the aperture, Fig. 55. All other members of this family, *Anredera cordifolia* (Nowicke, 1975: fig. 61), *Ullucus tuberosus* (Nowicke, 1975: fig. 62), and *Anredera scandens* (Nowicke & Skvarla, 1977: fig. 3) have the characteristic spinulose/punctate tectum of the order.

DIDIEREACEAE

The pollen of the Didiereaceae can be distinguished from all other Centrospermae by the apertures, 5–7 zonocolpate. This small family, four genera and ten species endemic to Madagascar, is characterized by a succulent habit, and successful grafting experiments with the Cactaceae supports the contention that these two families are closely related, regardless of the geographical distribution.

Based on the examination of three species representing two genera, *Alluaudia humbertii*, Figs. 11–12, 43, *A. procera* (Nowicke, 1975: figs. 66, 80; Skvarla & Nowicke, 1976: fig. 28), and *Decarya madagascariensis* (unpublished data) the pollen morphology, a spinulose and perforate tectum, confirms its inclusion in the Centrospermae by all recent generalists.

HALOPHYTACEAE

The Halophytaceae, a monotypic family in temperate South America, has a pollen morphology distinguished by a cubelike shape with a large pore on each of the six faces (Skvarla & Nowicke, 1976: fig. 3). In TEM (Skvarla & Nowicke, 1976: fig. 29) the structure of the exine is similar to some members of the Chenopodiaceae: a thick tectum supported by stout columellae on a thin foot layer underlain by a fragmented lamellar endexine. However, the sieve-tube plastid in the Halophytaceae has a globular central crystalloid in contrast to the Amaranthaceae and Chenopodiaceae, which lack this particular inclusion (Behnke, 1976). Since no other taxa examined thus far in the Centrospermae have pollen with this shape and aperture arrangement, we would agree with separate family status (Takhtajan, 1969).

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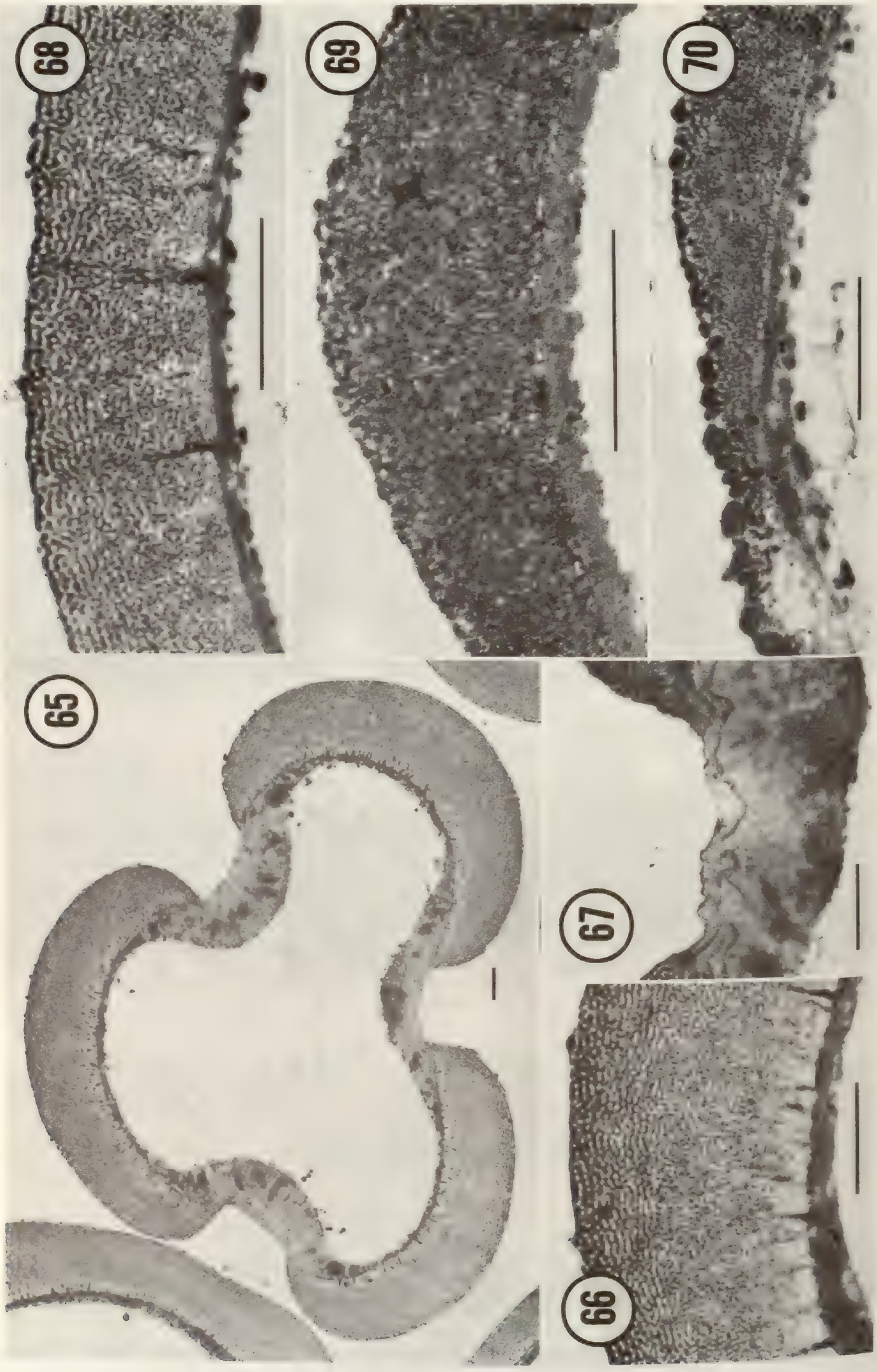
FIGURES 59–64. Scanning Electron Micrographs of Achatocarpaceae, Batidaceae, Gyrostemonaceae, and Theligonaceae pollen.—59. *Achatocarpus spinulosus* Grisebach (Achatocarpaceae), ×2,400.—60. *Theligonum cynocrambe* L. (Theligonaceae), equatorial view, ×2,310.—61. *Batis maritima* L. (Batidaceae), equatorial view, ×2,770.—62. *Gyrostemon australasicus* (Moq.) Heimerl (Gyrostemonaceae), polar view, ×2,310.—63. *Codonocarpus attenuatus* H. Walter (Gyrostemonaceae), equatorial view, ×1,850.—64. *Didymotheca pleiococca* F. Muell. (Gyrostemonaceae), polar view, ×2,160.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ACHATOCARPACEAE

Achatocarpus Triana and *Phaulothamnus* A. Gray are betalain genera which have been included in the Phytolaccaceae (Walter, 1909) or given separate family status as Achatocarpaceae (Heimerl, 1934; Eckhardt, 1964). According to Behnke (1976: figs. 6–7), both genera have the protein type of sieve-tube plastid characteristic of the centrospermous families. The presence of a globular central crystalloid eliminates a close tie to either Amaranthaceae or Chenopodiaceae, which lack this structure, and also to the Caryophyllaceae, which has a polygonal-shaped crystalloid.

The pollen morphology of *Achatocarpus* and *Phaulothamnus* is very similar: spheroidal shape, apertures consisting mostly of 4 to 6 large pores, but can be irregular, and a tectum which is scabrate (Bortenschlager et al., 1972; Nowicke, 1975: fig. 70) or very coarsely granular (unpublished data). The pollen is distinct from all other Centrospermae, but considering the range of variation in other families such as Nyctaginaceae, e.g., *Bougainvillea* (Nowicke, 1975: fig. 11), *Boerhaavia erecta*, Figs. 7–8, *Reichenbachia hirsuta*, Fig. 20; or Caryophyllaceae, e.g., *Cometes surattensis*, Fig. 17, *Siphonychia diffusa*, Fig. 26, *S. americana*, Fig. 27, *S. rugelii*, Fig. 32, *S. pauciflora*, Fig. 33, *Lychnis* (Nowicke, 1975: fig. 36); or Cactaceae (Nowicke, 1975: figs. 19–24), it would be difficult to justify the exclusion of *Achatocarpus* and *Phaulothamnus* from the Phytolaccaceae on this characteristic alone.

Only *Achatocarpus spinulosus*, Fig. 59, is illustrated in this paper.

THELIGONACEAE

Melchior (1964) included the Theligonaceae in the Myrtales near the Haloragaceae, and while Cronquist (1968) followed Melchior's suggestion, he also expressed some doubt as to the extent of the relationship between these two families.

The Theligonaceae have been the subject of several detailed investigations (Kapil & Mohana Rao, 1966; Praglowski, 1973; Wunderlich, 1971), but the classification remains controversial. The pollen morphology of *Theligonum cynocrambe*, Fig. 60, (3–)4–6(–7)-zonoporate with a tectum described as an illusory impression of a reticulum by Praglowski (1973), has no counterpart in all of the centrospermous taxa examined to date (see also Nowicke, 1975: figs. 71–72). This conclusion, together with the presence of anthocyanins and the starch type sieve-tube plastid, dismisses the possibility that the Theligonaceae are related to or derived from the Centrospermae. However, we have reservations about Wunderlich's (1971) proposal to treat *Theligonum* as a tribe in the Rubiaceae since neither the aperture condition nor the particular tectum as described above are known to occur in that family. In an unpublished study of 75 species in the tribe

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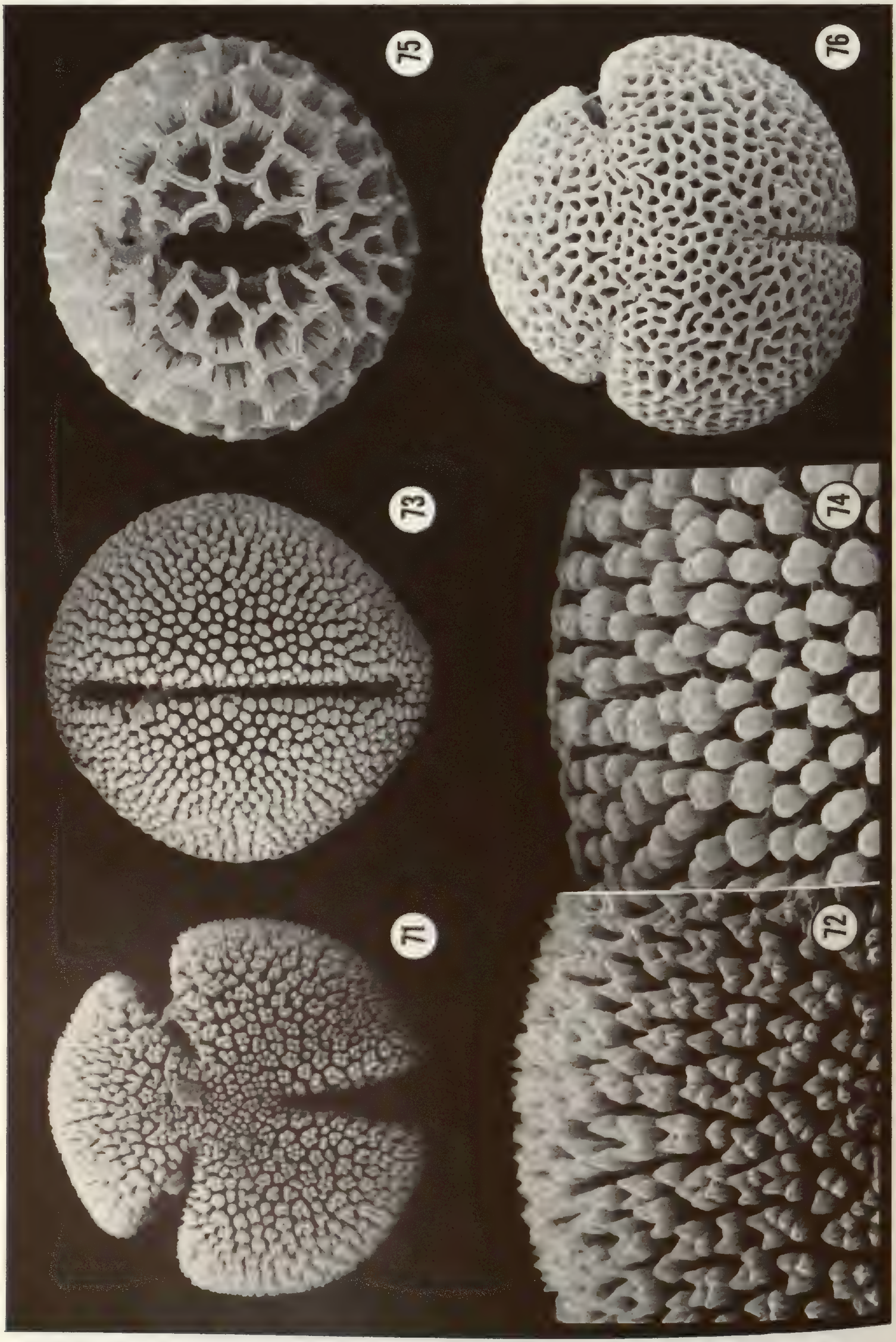
FIGURES 65–70. Transmission Electron Micrographs of Gyrostemonaceae and Batidaceae pollen.—65. *Didymotheca pleiococca* F. Muell. (Gyrostemonaceae), ×4,300.—66. *D. pleiococca*, ×15,580.—67. *D. pleiococca*, ×11,400.—68. *Codonocarpus cotinifolius* (Desf.) F. Muell. (Gyrostemonaceae), ×23,400.—69. *Batis maritima* L. (Batidaceae), ×30,400.—70. *B. maritima*, ×19,720.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Guettardeae and 16 in the Ixoreae, Nowicke found 3-porate grains in some species of *Guettardus,* but regards this condition as derived from 3-colporate due to a progression of intermediate forms. The 4–7-zonoporate aperture type found in *Theligonum* is another matter altogether. Furthermore, we are of the opinion that the tectum of the rubiaceous genera *Asperula, Athosperma,* and *Galium* (unpublished data) is not similar to that found in *Theligonum.*

Praglowski (1970), who described the pollen morphology of the Haloragaceae as well as Theligonaceae, did not consider the two families to be closely related. However, we are of the opinion that the Theligonaceae is more likely to be related to the Haloragaceae than to the Rubiaceae. At least the Haloragaceae has taxa with this aperture type (Praglowski, 1970: plate 7, fig. 2) and possibly even the tectum (Praglowski, 1970: plate 13, figs. e, f).

The only point on which all investigators seem to agree is the distinction of this small family of two or three species.

BATIDACEAE AND GYROSTEMONACEAE

The general agreement that neither the Batidaceae nor Gyrostemonaceae belong in the order Centrospermae is not surprising since both lack the betalains, both have the starch type sieve tube plastid, and each has a chromosome number other than the $x = 9$ for the centrospermous families: Batidaceae $x = 11$, and Gyrostemonaceae $x = 14$. The present controversy concerns the extent of their relationship to each other, if any, and their placement in the dicot hierarchy.

The Batidaceae consists of one genus and two species distributed along the tropical and subtropical littoral, mostly in the New World. Its superficial resemblance to the Chenopodiaceae, wiry stems, succulent leaves, small flowers, and its occupation of a similar habitat, probably initiated the idea of a relationship with the Centrospermae.

The Gyrostemonaceae, 5 genera and perhaps 20 species, is a family of small trees and shrubs endemic to Australia. The superficial resemblance of its female flowers to the free-carpelled members of the Phytolaccaceae may have prompted the early treatment as members of that family.

The dubious relationship between the Batidaceae and Gyrostemonaceae, seemingly initiated by their mutual inclusion and exclusion from the Centrospermae, received unwarranted support when transmission electron microscopy revealed an unstratified exine in each family (Figs. 65–70). The structure of the exine distinguishes the Gyrostemonaceae from all other dicots that have been examined in thin section. As illustrated in Figs. 65–68, the ektexine is unstratified and lacks the typical components, foot layer, columellae, and tectum. There are, however, certain characteristics which deserve mention: in the mesocolpus, Figs. 66 and 68, the endexine (nexine of Prijanto, 1970a) is thin and of a uniform

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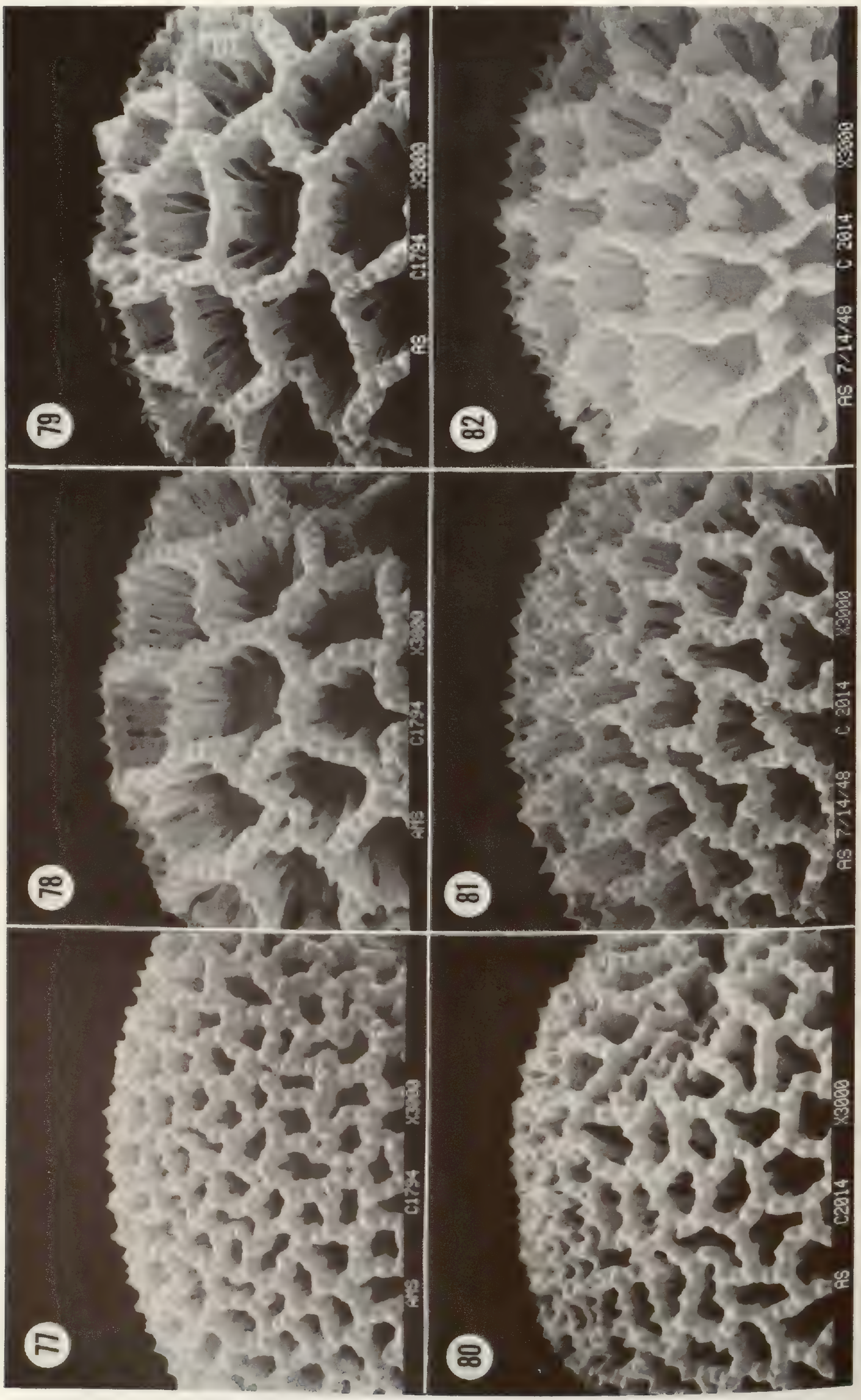
FIGURES 71–76. Scanning Electron Micrographs of Plumbaginaceae pollen.—71. *Ceratostigma griffithii* C. B. Clarke, polar view, pointed verrucae form, ×990.—72. *C. griffithii,* ektexine surface, ×3,550.—73. *C. griffithii,* equatorial view, rounded verrucae form, ×890.—74. *C. griffithii,* ektexine surface, ×3,550.—75. *Statice tenella* Turcz., equatorial view, coarsely reticulate form, ×1,140.—76. *S. tenella,* polar view, finely reticulate form, ×1,100.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density, whereas in the region of the colpus, Fig. 67, it is massive due mostly to an additional substance which is less electron dense; the ektexine is for the most part amorphous, but the extreme distal portion may be an exception, and the proximal part does have small, vertical elements distinguished by a greater electron density. These characteristics, although subtle, essentially agree with the earlier work of Prijanto (1970a).

In SEM all Gyrostemonaceae examined (Nowicke, 1975: figs. 67–69; Goldblatt et al., 1976: figs. 1A–1C; Behnke, 1977: figs. 10–14) are similar in aperture, 3-colpate with well-delimited colpi, and in the exine surface which varies only slightly from the psilate condition, e.g., *Gyrostemon australasicus*, Fig. 62, *Codonocarpus attenuatus*, Fig. 63, and *Didymotheca pleiococca*, Fig. 64.

Figure 61 is, to our knowledge, the first SEM of *Batis maritima* and illustrates an almost psilate (finely granular?) surface and a 3-colporoidate aperture condition.

Only one collection of *Batis maritima* (Table 1) was examined in thin section, Figs. 69–70, and the subtle differences found in the exine of Gyrostemonaceae were not apparent. These results agree with those of Prijanto (1970b).

Other similarities in pollen morphology between the two families include the aperture condition, 3-colpate or 3-colporoidate, and a psilate or granular exine surface. These characteristics are common in the dicots and their mutual presence does not, a priori, indicate a relationship, but they do not argue against one.

According to Eckhardt (1971) there are similarities in the inflorescences, and Mabry (1976) has reported the presence of glucosinolates in both families. The Batidaceae and Gyrostemonaceae have in common another characteristic more rare than the unstratified exine, and that is the absence of pigmented parts. These two families have neither anthocyanins nor betalains, a condition not found in the remaining dicots, to our knowledge.

There are striking differences between the two families: the Batidaceae are wiry herbs with opposite leaves, have female flowers consisting of two carpels, and seeds with a straight embryo and no endosperm; in contrast, the Gyrostemonaceae are shrubs or trees with alternate leaves, the female flowers have numerous carpels attached to a central column, seeds with a curved embryo and copious endosperm.

In view of the unusual similarities, it seems unwise to summarily dismiss the possibility of a relationship between the Batidaceae and Gyrostemonaceae. A reexamination of the floral and vegetative morphology of both families might clarify their relationship to each other and their position in the dicot hierarchy. Thorne's (1976) suggestion that the Gyrostemonaceae may be related to the wind-pollinated Australian Sapindaceae should be explored, since *Dodonaea* (unpublished data) has thick-walled grains. The male and female flowers in the Gyrostemonaceae do not have the characteristics or modifications associated with wind pollination.

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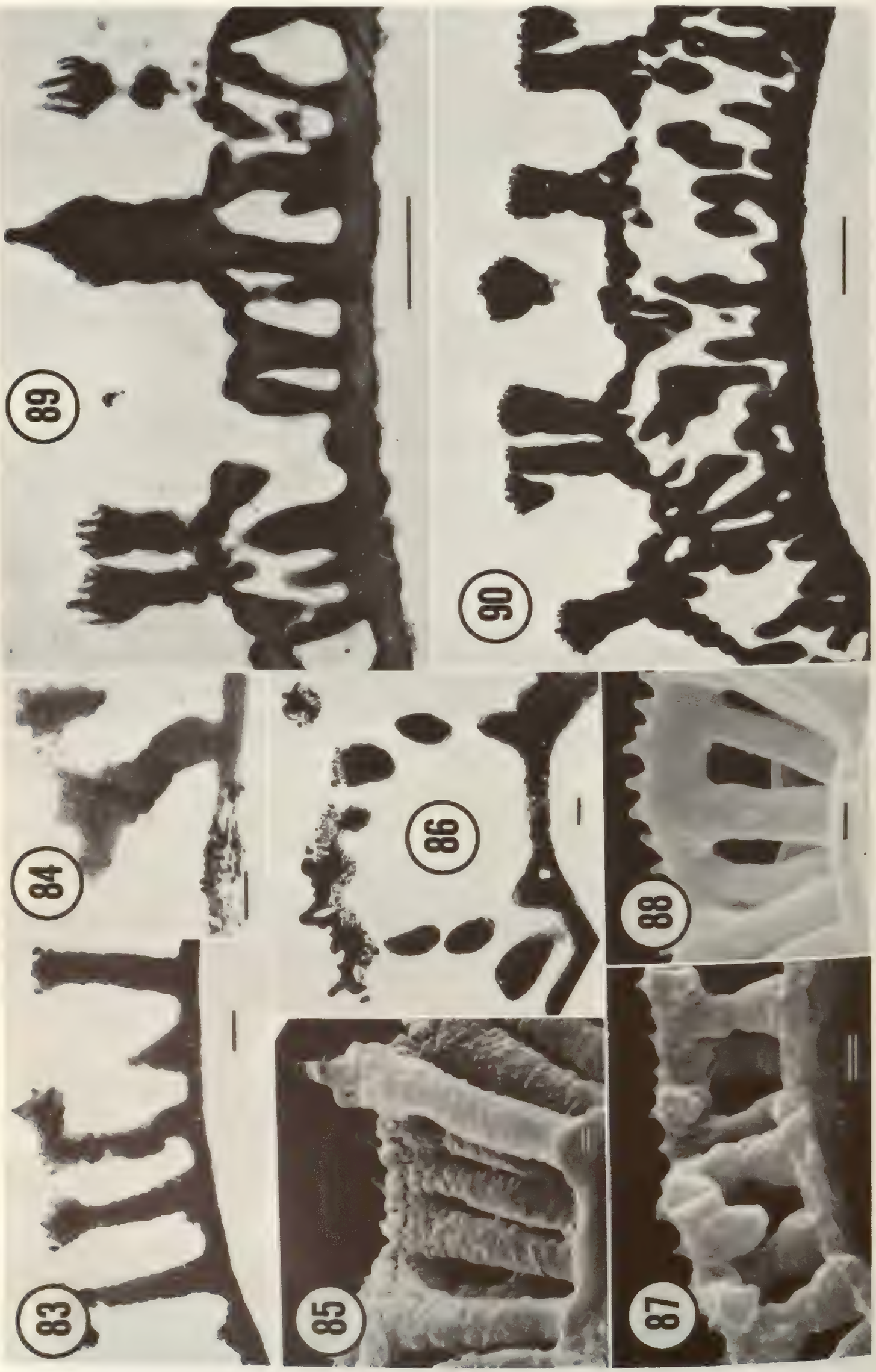
FIGURES 77–82. Scanning Electron Micrographs of the variation in the tectum of *Armeria maritima* var. *sibirica* (Turcz.) Lawrence (Plumbaginaceae), all ×2,010.—77–79. All from one inflorescense (*Cody 1794* US, Greenland).—80–82. All from one inflorescence (*Calder 2014* US, Canada). The identification system (alpha numerics) has been retained in Figs. 77–82.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The Orders Plumbaginales, Polygonales and Primulales

The accumulating data on the limited distribution of the betalains and the specialized protein type of sieve-tube plastid, as well as the close similarity of the pollen morphology, strongly suggest that the Centrospermae are a terminal group in the dicots. We believe that the ancestral stock of the Centrospermae separated very early from the main group of dicot predecessors, and that this line gave rise to only the cluster of betalain families and Caryophyllaceae and Molluginaceae, and to no other existing angiosperms. Despite the presence of the anthocyanins and the starch type sieve-tube plastid and the absence of perisperm storage tissue and curved embryo, the Polygonaceae, and to a lesser extent the Plumbaginaceae, are considered to be related to or derived from the Centrospermae. These two families, as well as the Primulaceae which has a free central placentation in common with the Centrospermae, formed the subject matter for the third study, "Pollen Morphology and the Relationship of the Plumbaginaceae, Polygonaceae, and Primulaceae to the Order Centrospermae" (Nowicke & Skvarla, 1977). In a comprehensive study that combined and integrated SEM and TEM, the pollen of 134 species in these three families was examined. The authors' conclusions, that the Plumbaginaceae, Polygonaceae, and Primulaceae are not related to nor derived from the Centrospermae, and that the three families are not related to each other, are documented with an extensive series of electron micrographs.

PLUMBAGINACEAE

The Plumbaginaceae has only two pollen types which Erdtman (1966) designated as the Armeria type and the Plumbago type, presumably for the genera in which he first found them. The most significant result in a systematic sense is the magnitude of the distinction between the two types: the Armeria type grains, Figs. 75–88, are 3-colpate, the tectum incomplete and of a reticulate configuration, the muri consist of a single row of columellae, the lumina represented by the foot layer, and lack free columellae (Nowicke & Skvarla, 1977: figs. 41–58, 65–68, 73–75, 77–81); the Plumbago type grains, Figs. 71–74, 89–90, are 3-colpate, rarely pantocolpate, the tectum complete, supporting verrucae placed singly or in small clusters (Nowicke & Skvarla, 1977: figs. 29–40, 59–64, 69–72, 76).

In TEM the difference appears muted, but the structural difference is just as significant if not more so than the exomorphology illustrated in SEM: the Plumbago type has a tectum which is complete, Figs. 89–90, while the tectum in the Armeria type, Figs. 83–88, consists only of the distal fusion of the sparsely placed columellae. In thin section the Plumbago type has a foot layer, columellae, and

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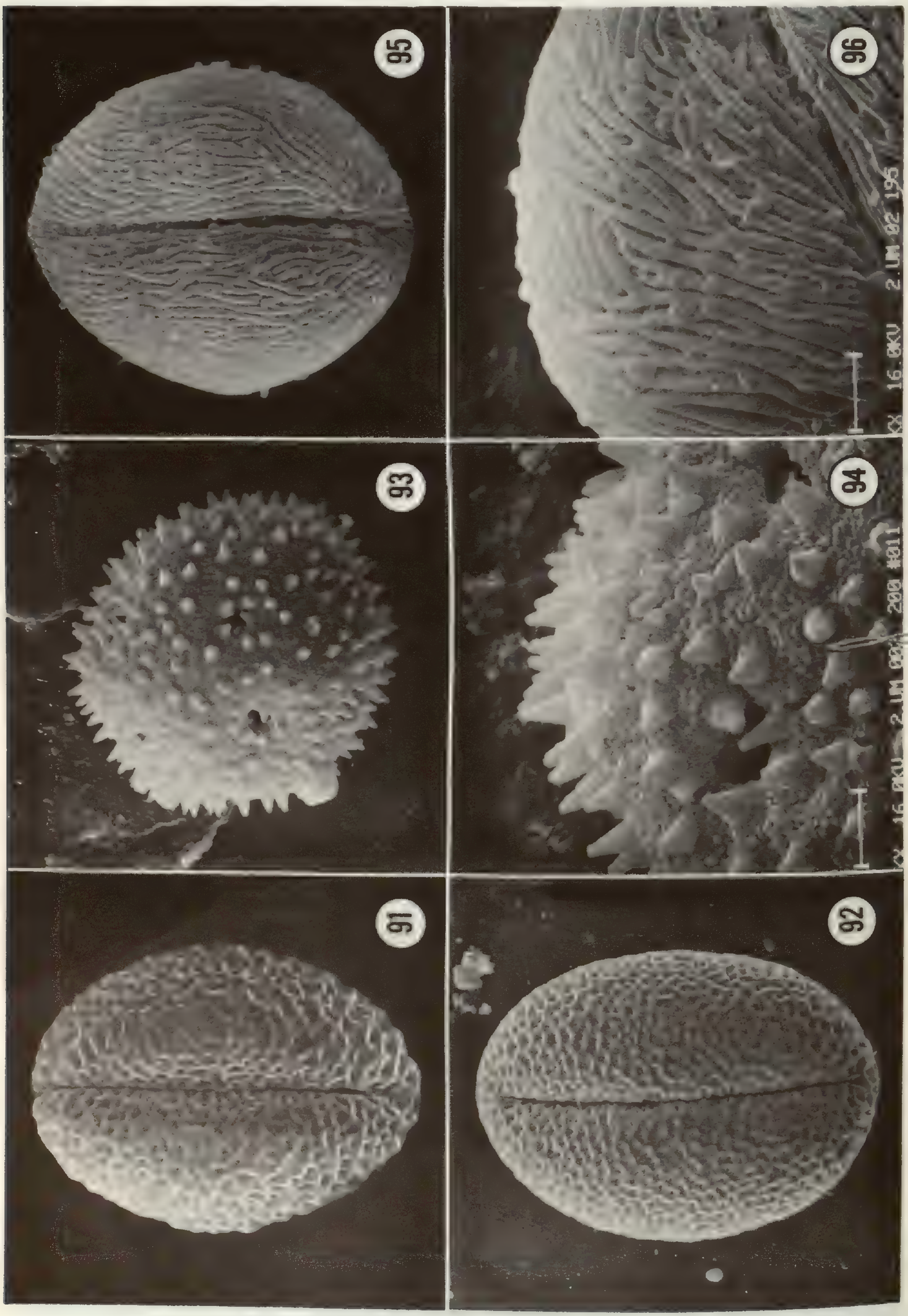
FIGURES 83–90. Transmission Electron Micrographs and Scanning Electron Micrographs of Plumbaginaceae pollen.—83. *Armeria maritima* (Miller) Willd., finely reticulate form, ×5,880.—84. *A. maritima*, finely reticulate form, aperture margin, ×6,440.—85. *A. maritima*, coarsely reticulate form, SEM of fractured grain, ×3,690.—86. *A. maritima*, coarsely reticulate form, ×3,640.—87. *Statice sinuata* L., finely reticulate form, SEM of fractured grain, ×6,500.—88. *S. sinuata*, coarsely reticulate form, SEM of fractured grain, ×5,000.—89. *Ceratostigma griffithii* C. B. Clarke, pointed verrucae form, ×15,080.—90. *C. griffithii*, rounded verrucae form, ×10,080.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an uneven but continuous tectum (any large gap is an artifact of preparation) on which the verrucae are placed. In constrast, the TEMs of the Armeria type illustrate a foot layer, some aspect of the columellae, and some aspect of the tectum, depending on the orientation of the section. With the possible exception of Fig. 84, the thin sections illustrated here do not demonstrate an endexine. Both types do have this layer, at least in the region of the apertures (Nowicke & Skvarla, 1977: figs. 65–66, 68, 71, 73–74, 77, 80–81).

Our interest in the Plumbaginaceae was and is the extent of its relationship to the Centrospermae; nevertheless, we take this opportunity to document an unusual result that was discussed in the previous study (Nowicke & Skvarla, 1977). Each of the two pollen types in the family has two forms: in the Armeria type there is a finely reticulate, Figs. 76, 83–84, 87, and a coarsely reticulate, Figs. 75, 85–86, 88, form; in the Plumbago type there is a pointed verrucae, Figs. 71–72, 89, and a more rounded verrucae, Figs. 73–74, 90, form. *Armeria maritima* var. *sibirica* has been described as monomorphic (Baker, 1966; Philipp, 1974), i.e., having only one type of stigma and only one form of the Armeria type pollen, that with the coarsely reticulate tectum. Using samples only from collections made between longitude 30° West and 60° East, Praglowski & Erdtman (1969) found six pollen forms, and as many as four in a single anther. Material from this particular geographic region was not available, but we did examine five collections from Greenland and one from Canada (see Table 3, Nowicke & Skvarla, 1977). Anthers were removed from one inflorescence from each collection. All six consisted of mixtures of the finely and coarsely reticulate Armeria forms, moreover, the distinction of the two forms was diluted and the coarsely reticulate form was predominant. Figures 77 through 82 illustrate the range of variation found in two of the collections, *Cody 1794* from Greenland, Figs. 77–79, and *Calder 2014* from Canada, Figs. 80–82. All six micrographs were taken at an original magnification of ×3,000: in the Greenland collection, Figs. 77 and 79 could be classified as the finely and coarsely reticulate forms, respectively, with Fig. 78 representing only a slight variant of the coarsely reticulate form; on the other hand, the micrographs of three grains from the Canadian collection, Figs. 80–82, are all intermediate in the size of the lumina. Any comments on the origin or adaptive significance of this phenomenon by us would be speculative, and we bequeath the problem to the reproductive strategists and field botanists. The following quote (Nowicke & Skvarla, 1977: p. 8) still applies: "The existence of heterostyly and dimorphic pollen grains in the Plumbaginaceae, however, in no way detracts from the conclusion of this study: None of the pollen examined in the Plumbaginaceae is similar or related to the common type found in the Centrospermae."

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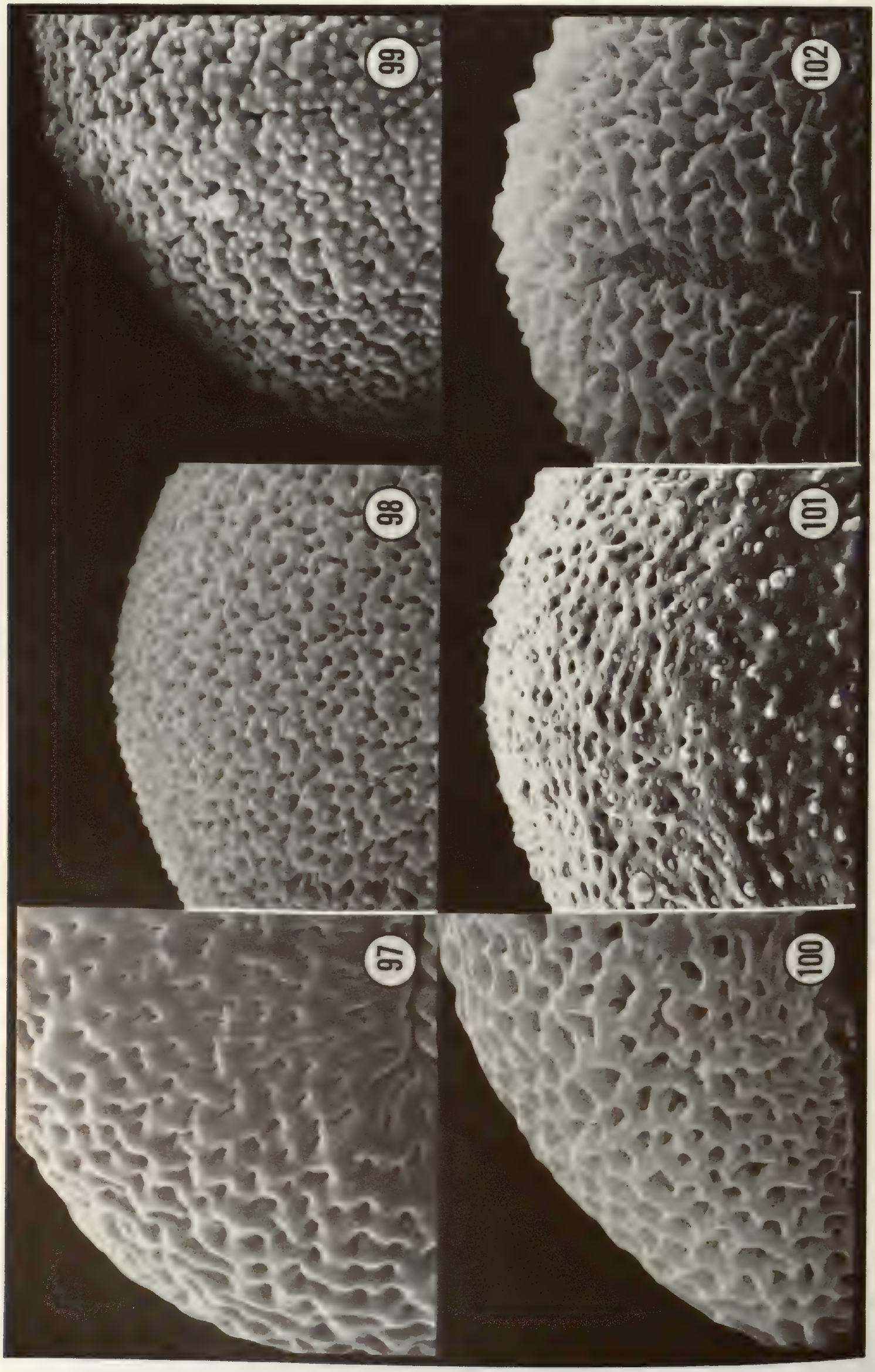
FIGURES 91–96. Scanning Electron Micrographs of Polygonaceae pollen.—91. *Muehlenbeckia polybotryar* Meisn., equatorial view, ×2,230.—92. *Fagopyrum cymosum* (Trev.) Meisn., equatorial view, ×1,240.—93. *Koenigia islandica* L., ×2,080.—94. *K. islandica*, ektexine surface, ×5,780.—95. *Atraphaxis spinosa* L., equatorial view, ×2,590.—96. *A. spinosa*, ektexine surface, ×5,780. In Figs. 94 and 96 the identification system has been retained, and the magnification bar equals 2 μm.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POLYGONACEAE

There is almost complete agreement that the Polygonaceae are a well-defined and easily recognized family, the sheathing leaf bases, small trimerous flowers, an undifferentiated perianth, and winged nutlets are easy field markers. Neither the size, 40 genera and 800 species, nor the floral morphology, unspecialized (reduced?), can explain the range of variation in pollen morphology in the Polygonaceae, Figs. 91–124 (Nowicke & Skvarla, 1977: figs. 82–173). The significance of this diversity, especially the origin, is of great interest itself, but for the purpose of this review the conclusion, based on 85 species from the previous study (Nowicke & Skvarla, 1977) and 15 additional species, remains: none of the taxa examined had a pollen morphology similar to the common type in the Centrospermae.

The apertures in the Centrospermae are all simple, whereas in the Polygonaceae compound apertures predominate. In LM the endoapertures are well defined, and the zonorate ones are often strikingly distinct due to the thickened margins. The 3-colporate aperture is the most common type but pantoporate types are also well represented.

The tectum varies widely, from forms which are almost complete or continuous, except for sparsely distributed punctae (Nowicke & Skvarla, 1977: figs. 82, 84), to those in which the tectum is incomplete, represented only by the distal union of major columellae, *Polygonum amphibium*, Fig. 105, *P. orientale*, Fig. 108 (Nowicke & Skvarla, 1977: figs. 112–123). The most common form is punctate-striate, in which the punctae are connected by thin grooves designated as striae, *Muehlenbeckia polybotryar*, Fig. 91, *Fagopyrum cymosum*, Fig. 92, and *Chorizanthe paniculata*, Fig. 97 (Nowicke & Skvarla, 1977: figs. 88–105). In some taxa the striae are longer and deeper, producing an uneven surface consisting of "outpockets" of tectum, as in *Ruprechtia pallida*, Fig. 102, and related species (Nowicke & Skvarla, 1977: figs. 106, 108–109). The tectum of *Podopterus mexicanus*, Fig. 100, has been described as microreticulate, but this designation, like so many others, is an arbitrary one.

In thin section all of the taxa examined in the Polygonaceae have the exine stratification considered as typical of the dicots, endexine, foot layer, columellae, and tectum. However, differences in the development of each of these units have produced a variation in the structure of the exine, Figs. 109–124 (Nowicke & Skvarla, 1977: figs. 142–173) that rivals the variation in exomorphology, Figs. 91–108 (Nowicke & Skvarla, 1977: figs. 82–141). The thin sections of *Chorizanthe paniculata*, Fig. 120, *Muehlenbeckia polybotryar*, Fig. 115, and *Ruprechtia pallida*, Fig. 124, can be considered as representative of the most common tectum, punctate-striate (see also Nowicke & Skvarla, 1977: figs. 144–145, 152–153, 171, 173). *Polygonum amphibium*, Fig. 112, and *P. orientale*, Fig. 113, are from taxa with an incomplete or reticulate tectum. Both are radial sections and each illus-

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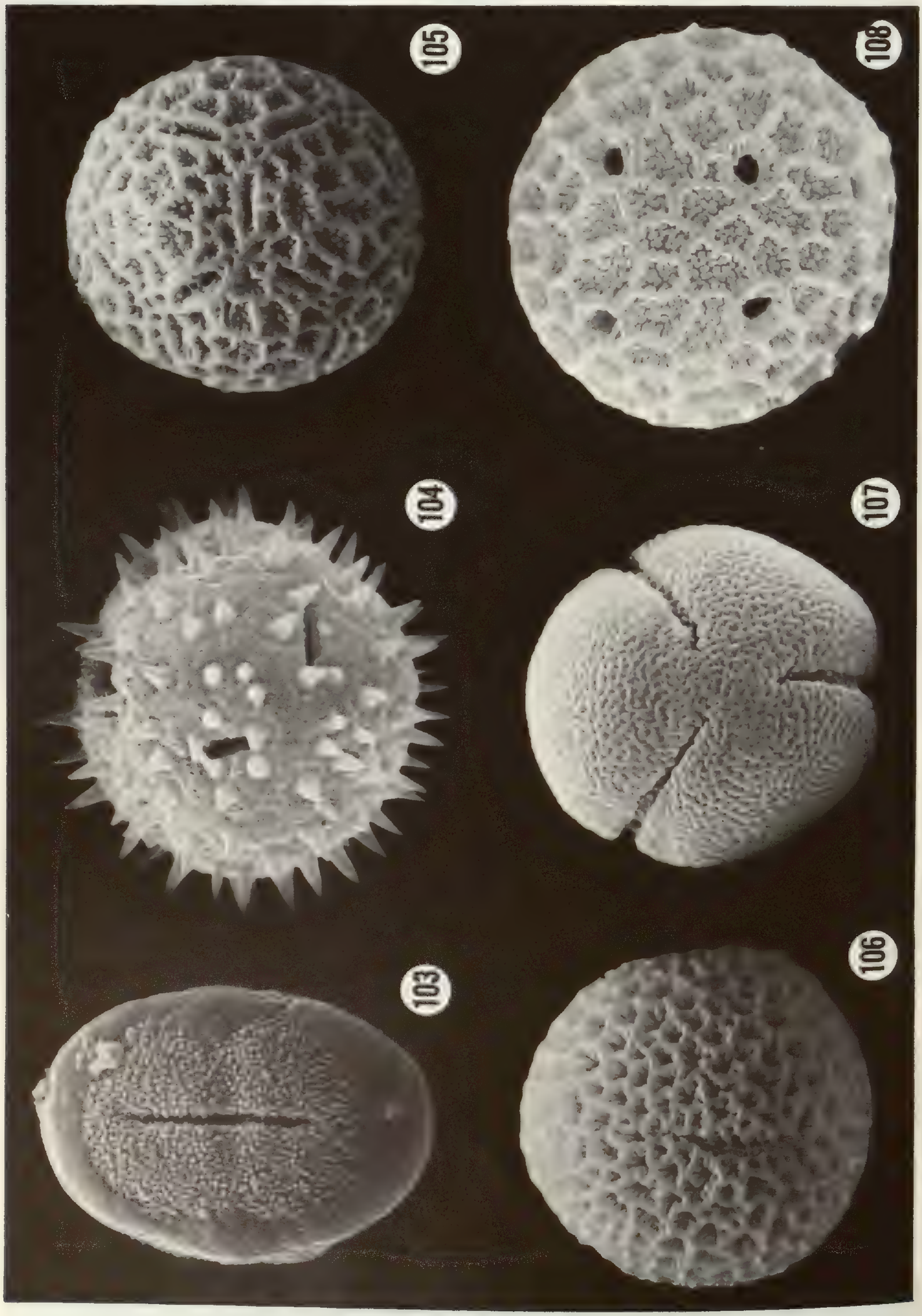
FIGURES 97–102. Scanning Electron Micrographs of ektexine surfaces of Polygonaceae pollen, all ×5,780.—97. *Chorizanthe paniculata* Benth.—98. *Emex australis* Steinheil.—99. *Rumex scutatus* L.—100. *Podopterus mexicanus* H. & B.—101. *Polygonum vaccinifolium* Wall.—102. *Ruprechtia pallida* Standl.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trates several views of columellae. In Fig. 113, from the pore at the extreme left (note fragment of endexine), the cut is parallel with the long axis of a murus, across a lumina with free columellae, then at a right angle to the long axis of another murus revealing the double row of columellae construction (this is less clear in Fig. 112 due to the slightly oblique angle). The thin section of *Podopterus mexicanus*, Fig. 121, is consistent with the morphology depicted in SEM, Fig. 100. The subfamily Eriogonoideae has a tectum in which the inner surface is granular, illustrated here by *Chorizanthe paniculata*, Fig. 120 (see also Nowicke & Skvarla, 1977: figs. 145–146, 149, 157–158).

The following discussions of specialized morphologies integrate the data from LM, SEM, and TEM.

In *Polygonum convolvulus*, Figs. 103 and 109 (Nowicke & Skvarla, 1977: figs. 140–141, 165) and related species, *P. cristatum* and *P. dumetorum*, and also in *Polygonella fimbriata* (Nowicke & Skvarla, 1977: figs. 130, 161) and related species, the tectum is dimorphic: one type outlining the colpi and another type on the mesocolpial ridges and at the poles. Figure 109 is a section at a right angle to the long axis of the grain: the endexine is concentrated mainly under the echinate type which outlines the colpi, and between these two areas is the mesocolpus with the psilate tectum. All of these taxa have a zonorate endoaperture with thickened margins.

Only three species of the approximately 100 examined in this family have pollen with a prominently spinulose tectum: *Koenigia islandica*, Figs. 93–94, 117, *Polygonum forrestii*, Figs. 104, 110 (Nowicke & Skvarla, 1977: figs. 133, 167), and *P. cyanandrium* (Nowicke & Skvarla, 1977: figs. 134–135). *Koenigia* and *P. cyanandrium* are pantoporate but some pores in *Koenigia* grains are distorted; *P. forrestii* is pantocolpate. In thin section, *K. islandica*, Fig. 117, and *P. forrestii*, Fig. 110, are very similar: the spines are the only well-defined component; all others, the foot layer, and especially the columellae, as well as the inner and outer surfaces of the tectum, are irregular and poorly defined. The restricted occurrence of this pollen morphology in the Polygonaceae suggests that these species are closely related (for discussion see Hedberg, 1947).

Only the *Bistorta* complex of *Polygonum*, illustrated here by *P. vaccinifolium*, Fig. 101 (Nowicke & Skvarla, 1977: figs. 124–129) had a tectum which could be described as sparsely spinulose and punctate. The unique structure revealed by thin section, however, dismisses any possibility that these taxa represent a link to the Centrospermae. In Fig. 114, a TEM of *P. vaccinifolium*, the slightly oblique angle detracts from the compacted columellae condition (see also Nowicke & Skvarla, 1977: figs. 164, 168), which distinguishes this group from all other members of the Polygonaceae and from all taxa examined to date in the Centrospermae.

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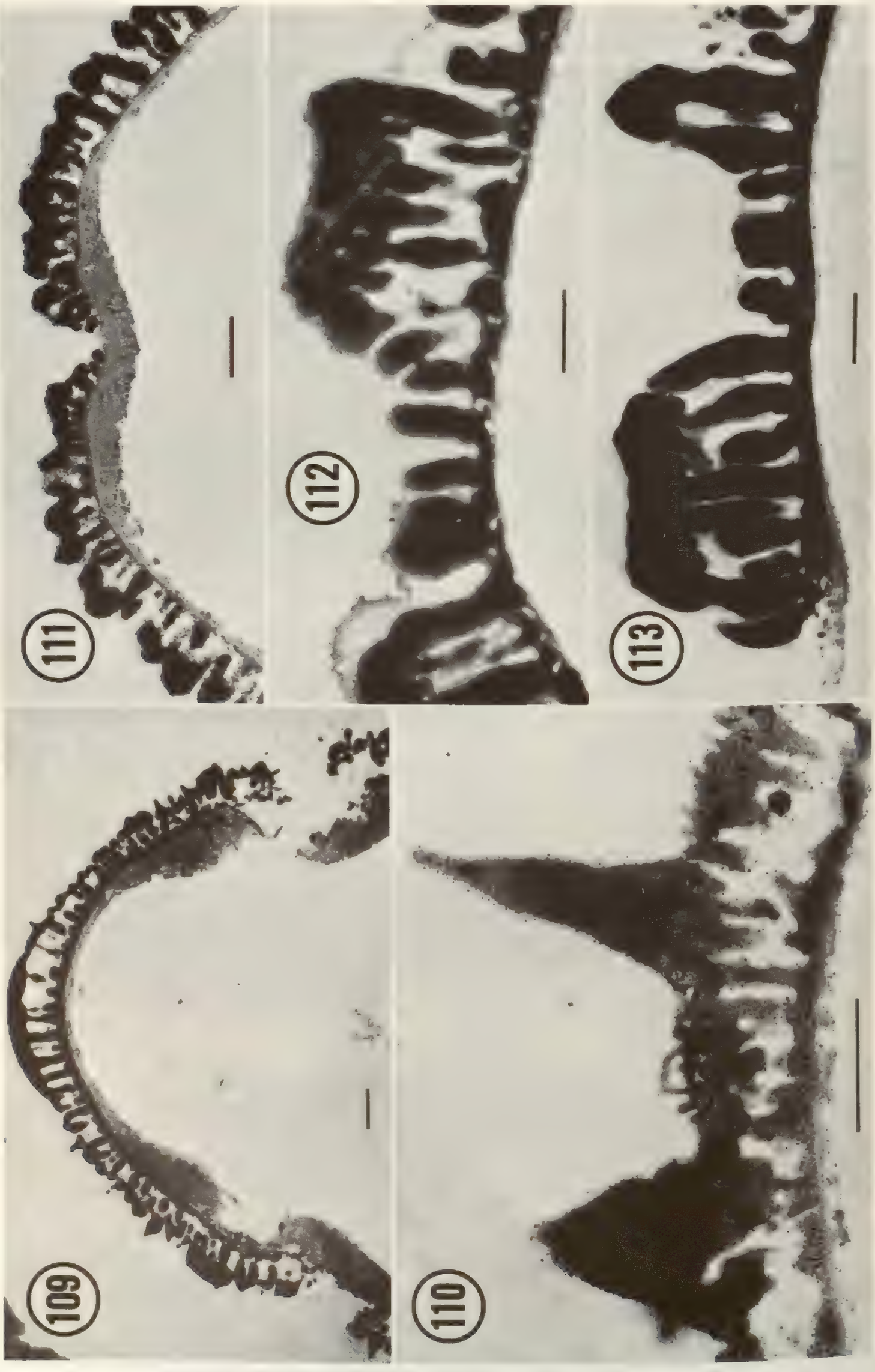
FIGURES 103–108. Scanning Electron Micrographs of *Polygonum* pollen.—103. *Polygonum convolvulus* L., equatorial view, ×2,240.—104. *P. forrestii* Diels, ×2,290.—105. *P. amphibium* L., ×1,160.—106. *P. glaciale* (Meisn.) Hook. f., equatorial view, ×1,870.—107. *P. cilinode* Michx., polar view, ×2,370.—108. *P. orientale* L., ×1,260.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Two genera, *Emex* and *Rumex*, illustrated here by *E. australis*, Fig. 98, and *R. scutatus*, Fig. 99, have a perforate and spinulose tectum in which the spinules are very small and evenly distributed. Comparison of thin sections of *Emex australis*, Figs. 122–123, with those of *Rumex acetosa* (Nowicke & Skvarla, 1977: fig. 170), a thick tectum supported by short, irregular columellae, a questionable foot layer, and an endexine which is exceptionally narrow (except in the aperture, Fig. 123), agrees with the close similarity depicted in SEM, Figs. 98–99, and supports their close relationship on other bases. The remarkably smooth or uniform inner surface of the tectum, Figs. 122–123, is perplexing but the oblique angle of section could, at least in part, produce this effect.

Four of the species examined since the 1977 paper are illustrated here. *Atraphaxis spinosa* has the most conspicuously striate tectum, Figs. 95–96, of all Polygonaceae thus far. In thin section, Figs. 118–119, it is similar to *A. buxifolia* (Nowicke & Skvarla, 1977: fig. 143): both have a well-developed endexine, uneven foot layer, and irregular columellae. *Fagopyrum cymosum*, Fig. 92, is similar to *F. esculentum* (Nowicke & Skvarla, 1977: figs. 87, 150), the latter species is illustrated here in thin section, Fig. 116. *Polygonum cilinode* has a finely punctate-striate tectum, Fig. 107, and is distinguished in thin section, Fig. 111, by the apparent absence of a foot layer. *Polygonum glaciale*, Fig. 106, is from the Asian section *Cephalophilon*, all of which have reticulate ektexines. The size of the pollen and the characteristics of the muri and lumina vary within a sample (Nowicke & Skvarla, unpublished data).

PRIMULACEAE

The basis for the relationship between the Primulaceae and the Centrospermae is the presence of free central placentation. However, this similarity is now regarded as an example of parallel evolution or of independent origin, since no other characteristic, including pollen morphology (Nowicke & Skvarla, 1977: figs. 174–200), supports this view. Figures 125–130 could be considered as representative of aperture and tectum variation. *Coris monspeliensis*, Fig. 125, *Anagallis linifolia*, Fig. 126, *Glaux maritima*, Fig. 128, and *Naumbergia thyrsiflora*, Fig. 129, are 3-colpate, while *Cortusa matthioli*, Fig. 127, is a restricted aperture type in which the colpi fuse at the poles forming a triangular apocolpial field. *Primula officinalis*, Fig. 130, is 5–8-zonocolpate. The tectum ranges from finely granular, Fig. 127, to perforate, e.g., Figs. 126, 129, 133. Figure 125 is probably a perforate tectum obscured by a residue of pollenkitt. The lack of agreement in Fig. 128 of *Glaux maritima* with that in an earlier study (Nowicke & Skvarla, 1977: fig. 190) is probably a manifestation of heterostyly and dimorphic pollen (for discussion see Nowicke & Skvarla, 1977).

In thin section most Primulaceae pollen have an identifiable endexine, such as that in *Coris monspeliensis*, Fig. 131, *Glaux maritima*, Fig. 132, *Anagallis*

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FIGURES 109–113. Transmission Electron Micrographs of *Polygonum* pollen.—109. *Polygonum convolvulus* L., ×5,300.—110. *P. forrestii* Diels, ×18,240.—111. *P. cilinode* Michx., ×8,510.—112. *P. amphibium* L., ×11,020.—113. *P. orientale* L., ×9,890.

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linifolia, Fig. 133, and *Naumbergia thyrsiflora*, Fig. 134. *Cortusa matthioli*, Figs. 135–136, *Primula officinalis*, Fig. 137 (Nowicke & Skvarla, 1977: fig. 198) and *P. veris* (Nowicke & Skvarla, 1977: fig. 200) can be distinguished by the absence of a foot layer and the correspondingly enhanced endexine.

The Order Ranunculales

The very restricted distribution of both betalains and the protein type sieve tube plastid suggest that the centrospermous ancestors separated from the main stock early in the phylogenetic history of the dicots. If this tenet is accepted, the families which might share a common ancestry are most likely the "lower dicots" and the order Ranunculales is the logical starting point.

Most authors (Cronquist, 1968; Hutchinson, 1959; Takhtajan, 1969; Thorne, 1968) regard the Ranunculales as a primitive or at least unspecialized group of families. For the most part we follow Cronquist's concept of the order which includes the Ranunculaceae, Circaeasteraceae, Berberidaceae, Lardizabalaceae, Menispermaceae, Coriariaceae, Corynocarpaceae, and Sabiaceae.

Unlike the Centrospermae, in which the vast majority of the taxa in the betalain families and in the anthocyanin containing Caryophyllaceae and Molluginaceae had a very similar pollen morphology, the results from this investigation of the order Ranunculales do not support a close relationship between the Ranunculaceae, Berberidaceae, Lardizabalaceae, Coriariaceae, or Corynocarpaceae. (We are aware that a narrow interpretation of the pollen data might well reduce the order Ranunculales to the family Ranunculaceae.)

The discussions of these five families, however briefly presented here, are nonetheless based on examination of almost 200 species. Only the Berberidaceae and Ranunculaceae are illustrated by representative taxa in SEM and TEM.

RANUNCULACEAE

For a large family, 45 to 50 genera and more than 1,000 species, the pollen morphology of the Ranunculaceae is remarkably uniform. Even more remarkable is the fact that the only exceptions to a spinulose and punctate/perforate tectum were found in *Helleborus*, e.g., *H. viridis*, Figs. 164–165, *Hydrastis* (see the following discussion of Berberidaceae), *Paeonia*, e.g., *P. brownii*, Figs. 160–161, and *Trollius* e.g., *T. acaulis*, Figs. 162–163. The first three are controversial genera frequently separated from the Ranunculaceae, and the very distinctive tectum of *Trollius* may well be linked to isolating mechanisms of geographical location and self-fertilization. Certainly these two factors help to maintain this distinction.

All of the remaining taxa examined, 38 genera and 111 species, have a spinulose and perforate tectum. Representative species illustrated in SEM are:

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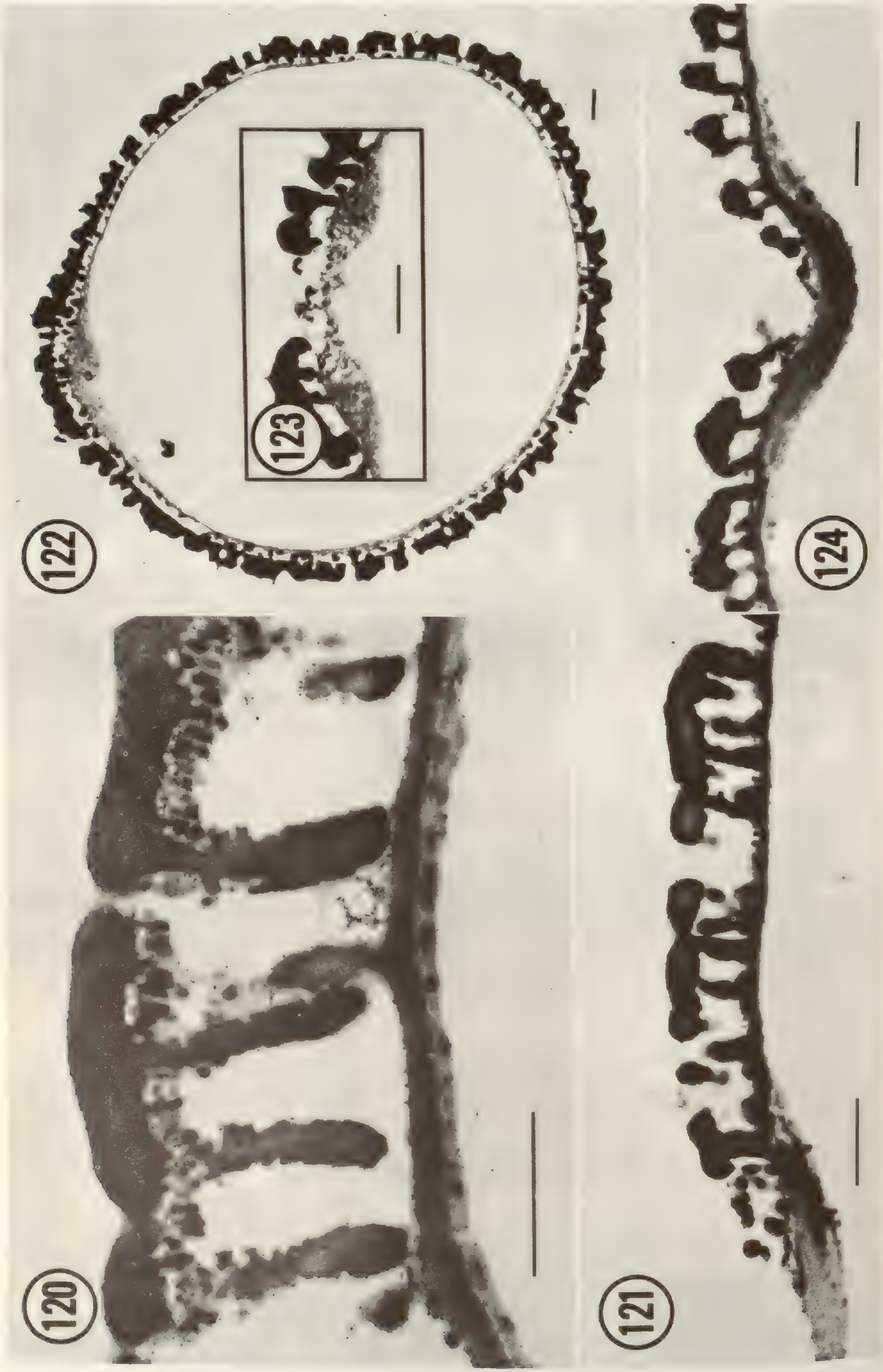
FIGURES 114–119. Transmission Electron Micrographs of Polygonaceae pollen.—114. *Polygonum vaccinifolium* Wall., ×13,050.—115. *Muehlenbeckia polybotryar* Meisn., ×13,050.—116. *Fagopyrum esculentum* Moench, ×14,210.—117. *Koenigia islandica* L., ×15,080.—118. *Atraphaxis spinosa* L., ×4,300.—119. *A. spinosa*, ×6,080.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Anemone coronaria, Fig. 149; *Ranunculus muricatus*, Fig. 150; *Coptis occidentalis*, Fig. 151; *Clematis orientalis*, Fig. 152; *Adonis pyrenaica*, Fig. 153; *Eranthis hyemalis*, Fig. 154. In numerous examples Ranunculaceae pollen was indistinguishable from various representatives of centrospermous families, particularly Amaranthaceae, Caryophyllaceae, and Chenopodiaceae. The range of variation in the size and distribution of spines and perforations in the Ranunculaceae was no greater than in some centrospermous families, e.g., Portulacaceae (Nowicke, 1975: figs. 16–17) or Nyctaginaceae (Nowicke, 1975: figs. 8, 12).

Thus far all taxa examined in the Ranunculaceae have simple apertures (*Paeonia* may be an exception): 3-colpate, e.g., *Clematis orientalis*, Fig. 152, *Adonis pyrenaica*, Fig. 153, and *Eranthis hyemalis*, Fig. 154; pantoporate, e.g., *Anemone coronaria*, Fig. 149, *Coptis occidentalis*, Fig. 151; pantocolpate, *Ranunculus muricatus*, Fig. 150. Other types not illustrated include: 5–8-zonocolpate, 6-pantocolpate, spiral, and irregular. The apertures are frequently variable within a sample, especially in the 3-colpate and 6-pantocolpate types. These grains do not appear sterile, i.e., their size and wall thickness is about the same as in grains with a more precise configuration of the apertures.

The close similarity depicted in SEM between the tectum of the Centrospermae and that of the Ranunculaceae is not paralleled in the structure of the exine. This is not to say that all taxa examined in the Ranunculaceae can be easily distinguished in thin section from the Centrospermae, but rather that some Ranunculaceae have modifications or developments not found in the pollen of the Centrospermae. One of the most consistent differences is the presence of an appreciable endexine in nonapertural regions, as well as beneath the apertures: in *Anemone coronaria*, Fig. 155, the endexine is massive and much thicker than either the foot layer or the tectum; in *Coptis occidentalis*, Fig. 159, the endexine is no doubt enhanced by the slightly oblique angle of section, but it would be prominent even in a perfectly radial section; *Clematis orientalis*, Fig. 156, *Ranunculus muricatus*, Fig. 157, and *Adonis pyrenaica*, Fig. 158, have a readily identified endexine layer. In most of the centrospermous taxa the endexine is usually present only in the region of the apertures.

Many taxa in the Ranunculaceae have modified columellae: larger in size and more sparsely distributed, or, very reduced and the tectum and foot layer scarcely separated. Grains of either type do have a distinctive exine structure. The former modification is illustrated here by *Anemone coronaria*, Fig. 155; it also occurs in species of: *Batrachium*, *Coptis*, *Hamadryas*, *Hepatica*, *Oreithales*, *Ranunculus*, and *Xanthorrhiza*. In the latter condition the columellae in *Adonis pyrenaica*, Fig. 158, and in *Glaucidium palmatum* (unpublished data), are reduced and are not the dominant component in cross-section. *Aconitum* (unpublished data) probably represents the extreme in columellae reduction and in *A. japonicum* only a thin broken line separates the tectum and the foot layer.

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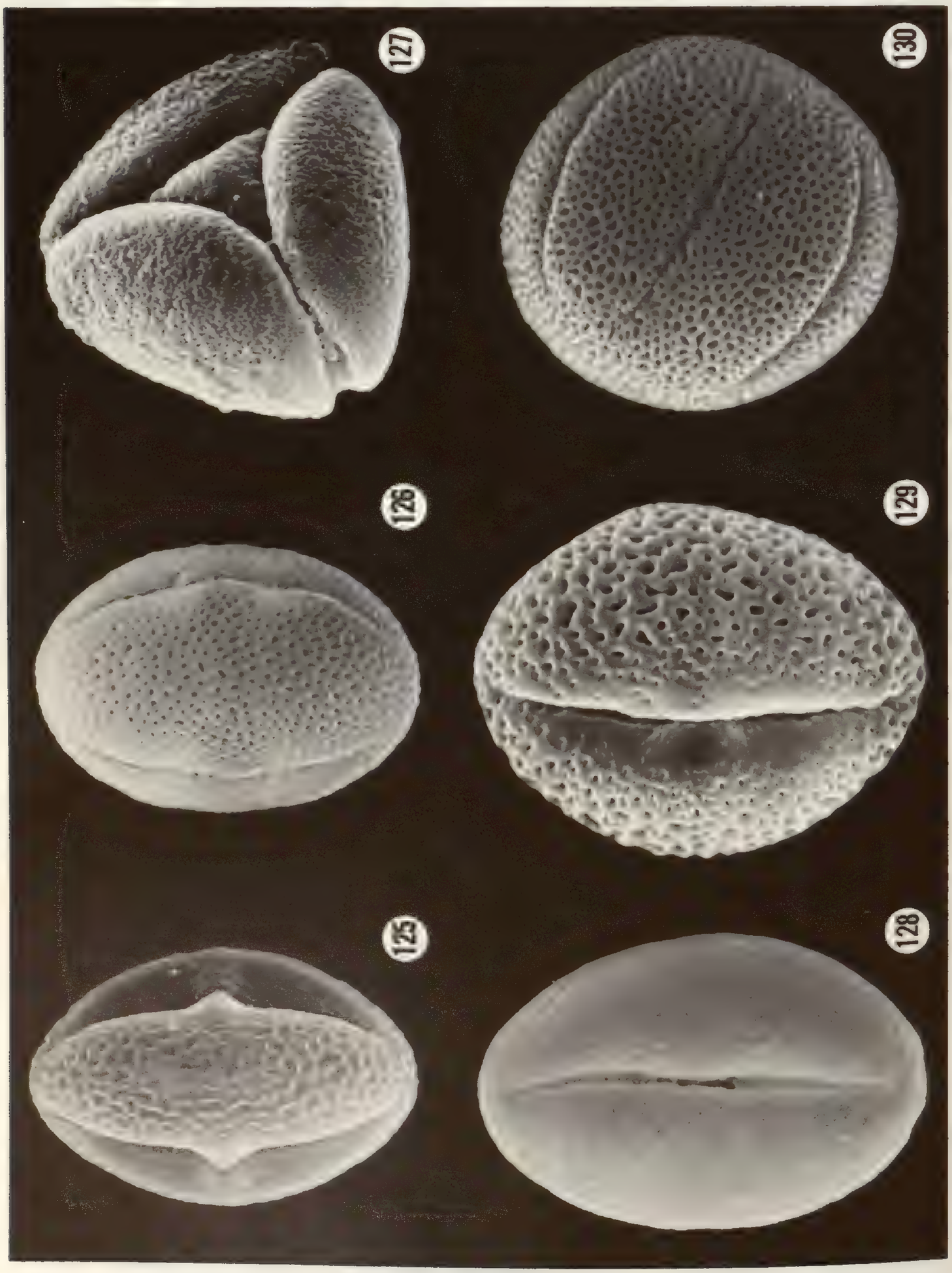
FIGURES 120–124. Transmission Electron Micrographs of Polygonaceae pollen.—120. *Chorizanthe paniculata* Benth., ×22,680.—121. *Podopterus mexicanus* H. & B., ×12,190.—122. *Emex australis* Steinheil, ×4,100.—123. *E. australis*, ×9,430.—124. *Ruprechtia pallida* Standl., ×8,510.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None of the Centrospermae examined in thin section have the extremes of columellae development which are found in the Ranunculaceae. Nevertheless, there are certain taxa in the Ranunculaceae which are indistinguishable in thin section from certain taxa in the Centrospermae.

Again, it is a peculiar distribution, an all or none phenomenon, which transforms a seemingly simple tectum into a significant characteristic: the Ranunculaceae is the first noncentrospermous family to have the spinulose and punctate/perforate tectum, and its presence in 111 of the 134 species examined argues compellingly that this family is the closest extant relative of the Centrospermae. Admittedly, neither the betalains nor the protein type sieve-tube plastid have been found in the Ranunculaceae, but it is the very restriction of these two features to the Centrospermae that makes the order unique. To make either or both a prerequisite for relationship to this unusual group of families defeats any investigation before it has begun.

BERBERIDACEAE

The traditional view of the Berberidaceae s.l. as a group of genera that are not closely related to each other is, in part, clarified and refined by the palynological data (Nowicke & Skvarla, 1979).

Berberis L. and *Mahonia* Nutt., illustrated by *B. fendleri,* Figs. 138, 144, and *M. nervosa,* Figs. 141, 145, have almost identical pollen, and this agrees with the close relationship or even congeneric treatment accorded the two genera on other bases. Of far greater significance than the expected similarity is the primitive state of the distinguishing characteristics: irregular apertures consisting of cracks or breaks, or spiral apertures in which the configuration of the furrows is not uniform even within a sample; the exine has an unspecialized or random surface, and psilate, punctate, punctate-striate, and granular can occur within a sample, and sometimes more than one on a single grain; in thin section, Figs. 144–145, the exine is amorphous and only the presence of irregular cavities indicates an early stage of stratification. This type of aperture, exine surface, and wall structure are uncompromisingly primitive and serve to isolate *Berberis* and *Mahonia* from all remaining ones. The woody habit, carpel structure, and chromosome number further distinguish these two genera, and we would agree with Hutchinson's (1959) restricted concept of the Berberidaceae as composed of only *Berberis* and *Mahonia*.

A sufficient pollen sample of *Ranzania japonica* (T. Ito) T. Ito, a relict species confined to the northern end of Honshu, was not obtained until March 1979. Briefly described, the grains are spherical, 6-pantocolpate, the surface unspecialized, and the exine unstratified in thin section.

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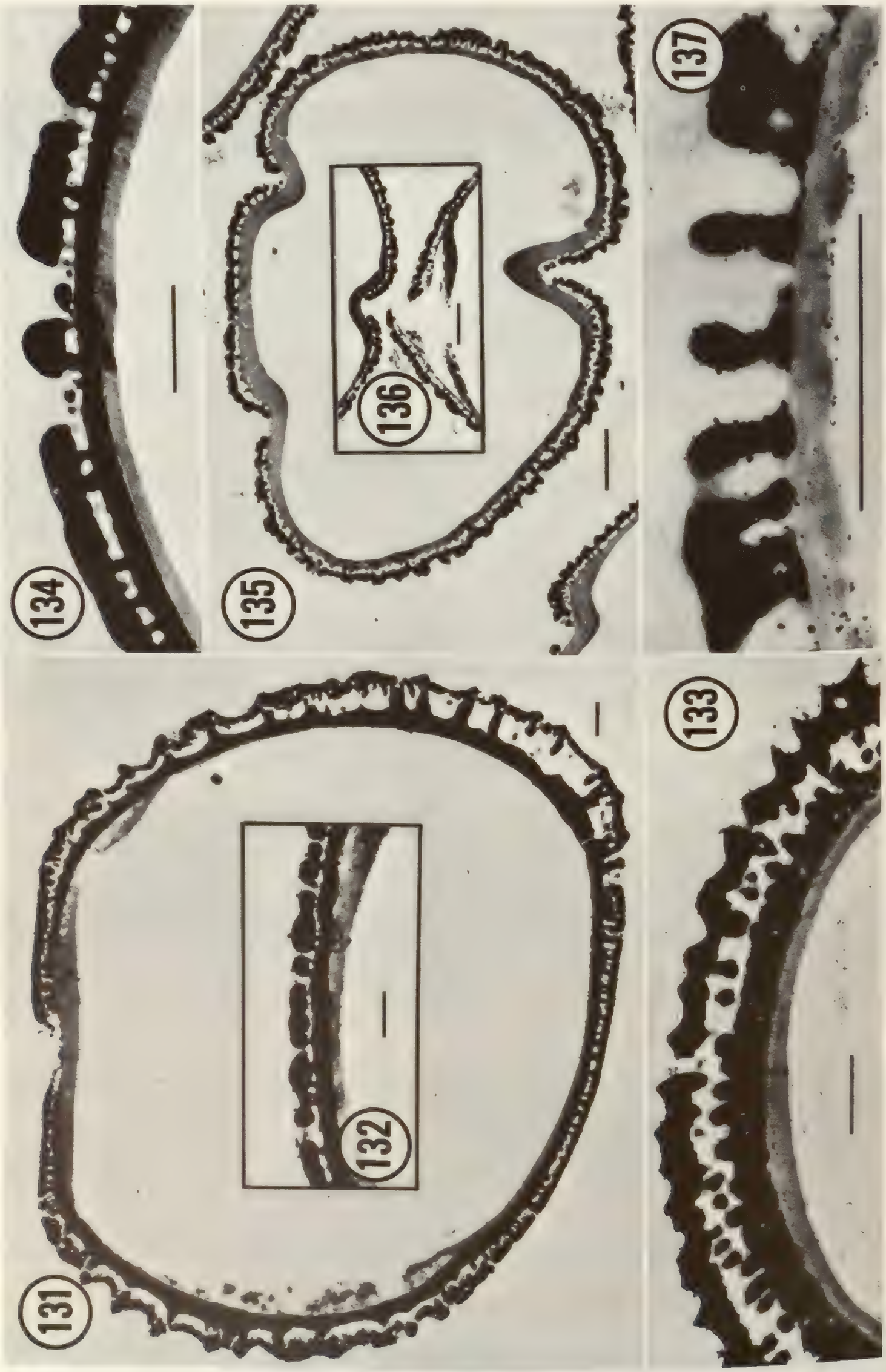
FIGURES 125–130. Scanning Electron Micrographs of Primulaceae pollen.—125. *Coris monspeliensis* L., equatorial view, ×1,800.—126. *Anagallis linifolia* L., equatorial view, ×2,925.—127. *Cortusa matthioli* L., oblique polar view with triangular apocolpial field, ×4,330.—128. *Glaux maritima* L., equatorial view, ×2,780.—129. *Naumbergia thyrsiflora* (L.) Reichenbach, equatorial view, ×3,680.—130. *Primula officinalis* (L.) Jacq., equatorial view, ×4,880.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None of the major United States herbaria had material of *Ranzania*, and specimens consisting of the only two collections at Kew were sent to the U.S. National Herbarium in April 1979. Although Terabayashi (1977, 1978) considers the floral morphology of *Ranzania* to be similar to that of *Berberis* and *Mahonia*, and all three have an unstratified exine, the great disparity in vegetative characteristics suggests that the ancestral stock of *Ranzania* separated very early from that of *Berberis-Mahonia*, and that the floral morphology of all three has remained unchanged. (For greater detail and photographs of the *Ranzania* herbarium specimens the reader is advised to consult Nowicke & Skvarla, 1979.)

Bongardia C.A. Meyer, *Caulophyllum* Michx., and *Leontice* L. are more closely related to each other than to any other berberidaceous genera in terms of pollen morphology. However, the unifying characteristics, grains which are larger and have a reticulate tectum, are scarcely the type to reinforce the separate family status accorded these genera by Airy Shaw (1966).

Nandina domestica Thunb. has been treated as a monotypic family by a number of workers, Takhtajan (1969), Airy Shaw (1966), and Kumazawa (1938). The pollen morphology is not particularly specialized, but the uniformly punctate tectum and a massive endexine distinguish this species from all other taxa in the Berberidaceae s.l. Thus the pollen lends support to those who favor separation of this genus on other characteristics.

The pollen morphology of the disjunct genus *Diphylleia* Michx., represented here by *D. sinensis*, Figs. 140, 148, is unique within the Berberidaceae, and within all of the order Ranunculales examined to date, but of itself has little systematic value. This same statement would apply to the pollen of *Podophyllum emodi*, tetrads that have a tectum of ripple-surfaced gemmae, which have, to our knowledge, no known counterpart in the dicots.

We are aware that in the genus *Podophyllum* L. the difference in pollen morphology between *P. emodi* and *P. peltatum* could be interpreted to be as great or greater than in the family as a whole.

For the remaining genera traditionally placed in the Berberidaceae the pollen data have strong implications regarding their relationships to each other, but admittedly not as definitive as in the case of *Berberis* and *Mahonia*.

The Old World genus *Epimedium*, with perhaps 25 species, has sufficient variation in the tectum to link the New World genus *Vancouveria*, both the Asian and American species of two disjunct genera, *Achlys* and *Jeffersonia*, illustrated by *J. diphylla*, Figs. 142, 147, *Dysosma pleianthum*, and *Podophyllum peltatum*, Figs. 139, 146. The primary or basic tectum consists of randomly distributed small rods with one end free and projecting slightly outward. The tectum in most of the above taxa has been modified principally by the loss of some of the distinction of the individual rods. In four species of *Epimedium*, *E. cremeum*, *E.*

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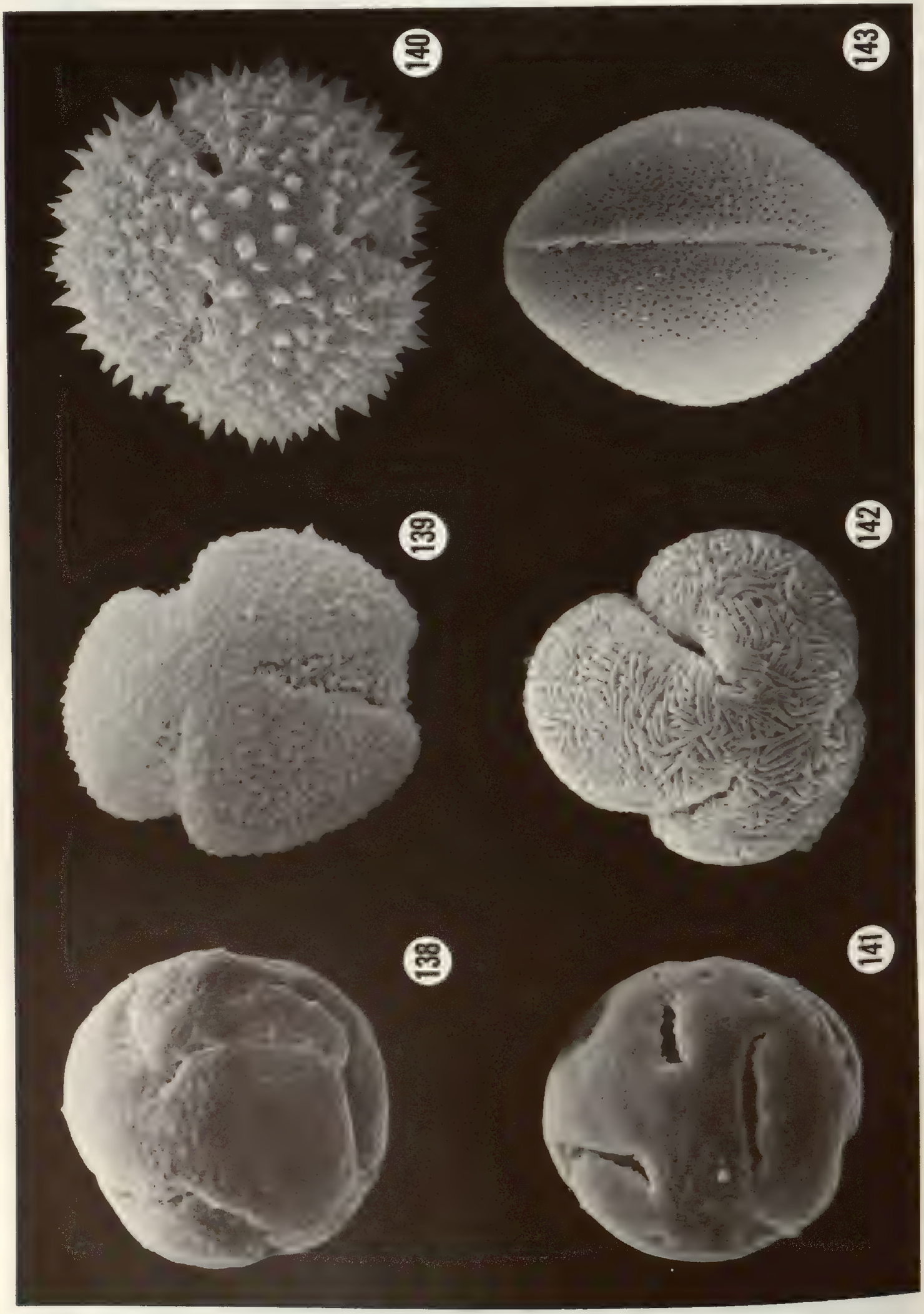
FIGURES 131–137. Transmission Electron Micrographs of Primulaceae pollen.—131. *Coris monspeliensis* L., ×5,040.—132. *Glaux maritima* L., ×6,840.—133. *Anagallis linifolia* L., ×11,040.—134. *Naumbergia thyrsiflora* (L.) Reichenbach, ×14,210.—135. *Cortusa matthioli* L., ×8,100.—136. *C. matthioli*, ×6,090.—137. *Primula officinalis* (L.) Jacq., ×41,650.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diphylla, *E. grandiflora*, and *E. sempervirens*, Fig. 143, and most collections of *P. peltatum*, there are grains in which the rods are still discernible. And, there are some grains in all four taxa in which five, six, or seven of the tips are arranged like the vanes of a pinwheel. The range of variation within each sample is such that an almost perfect continuum exists among the above four species (Nowicke & Skvarla, 1979).

The type of pollen morphology found in *Hydrastis* L. indicates that the genus is more closely related to the tribe Epimedieae than to any taxa in the Ranunculaceae. *Hydrastis* is one of the four genera in the Ranunculaceae which does not have a spinulose and punctate/perforate tectum, and the only one with a striate-reticulate tectum very similar to some species in *Epimedium* and *Vancouveria*. Dahlgren (1975) and Takhtajan (1969) treat *Hydrastis* as a monotypic family, while Airy Shaw (1966) includes the monotypic genus *Glaucidium* as well, citing features which link these two species to the Ranunculaceae on one hand and to the Berberidaceae on the other. But considering the distribution of the striate-reticulate tectum in the Ranunculales, we would place *Hydrastis* in the alliance of *Epimedium*, *Vancouveria*, *Jeffersonia*, and *Achlys*.

Glaucidium palmatum, which has been segregated with *Hydrastis* as either a family or subfamily in the Ranunculaceae, has 3-colpate grains with a punctate/spinulose tectum in which the punctae are sparsely distributed and the spinules are more numerous, and uniform in size and distribution. In both SEM and in TEM (unpublished data), the pollen is very similar to that of *Adonis pyrenaica*, Figs. 153 and 158. The pollen morphology does not indicate a close relationship with *Hydrastis*, nor would it reinforce the monotypic separate family status accorded by Dahlgren (1975) and Takhtajan (1969).

CORYNOCARPACEAE AND CORIARIACEAE

The following reports on the pollen morphology of the Corynocarpaceae and Coriariaceae are based on a very limited sample and should be considered with reserve, although our preliminary results do agree with those of Erdtman (1966).

The Corynocarpaceae, consisting of a single genus with five species distributed in the southwest Pacific (Australia, New Zealnd, New Caledonia, etc.), is only doubtfully referred to the Ranunculales by Cronquist (1968). The pollen of the one species available to this study, *Corynocarpus laevigata*, is sufficiently distinct to make it a key characteristic for the family's placement: the grains have a bilateral symmetry; the shape is extremely oblate in equatorial view; the apertures consist of two short, horizontal and opposite colpi; the surface is more or less psilate; in thin section the exine is relatively undifferentiated. Thorne (1976) placed the Corynocarpaceae in the order Rosales, suborder Cunoniinea,

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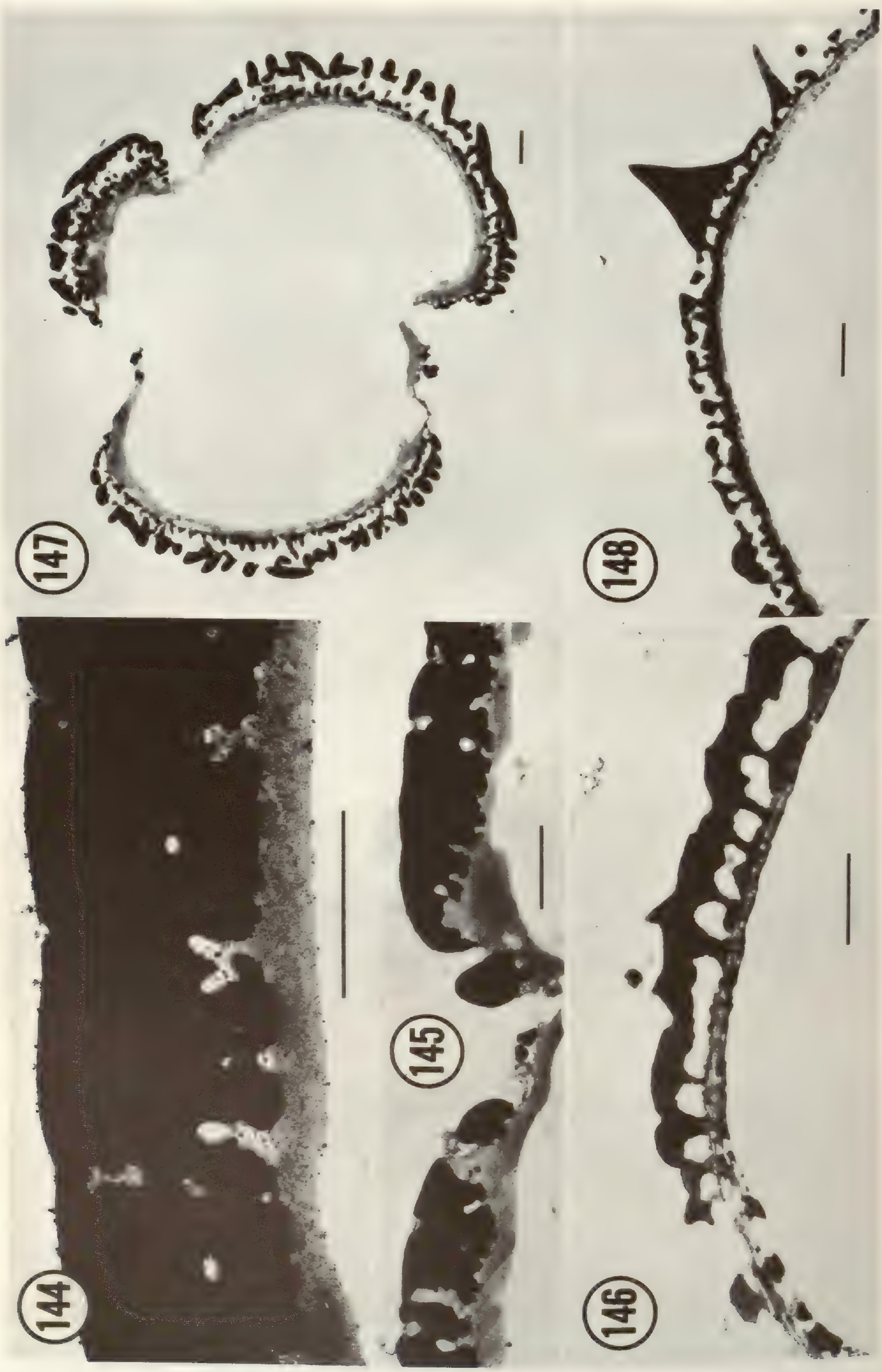
FIGURES 138–143. Scanning Electron Micrographs of Berberidaceae pollen.—138. *Berberis fendleri* A. Gray, ×1,420.—139. *Podophyllum peltatum* L., slightly oblique polar view, ×2,120.—140. *Diphylleia sinensis* Li, polar view, ×1,690.—141. *Mahonia nervosa* (Pursh) Nutt., ×980.—142. *Jeffersonia diphylla* (L.) Pers., slightly oblique polar view, ×2,460.—143. *Epimedium sempervirens* Nakai, equatorial view, ×2,125.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and adjacent to the Staphyleaceae. At this time, any comments about the relationships and affinities of Corynocarpaceae would be speculative.

The pollen morphology found in the Coriariaceae does little to clarify its systematic relationships except, perhaps, to interpret the distinction from all other taxa examined as evidence that it does not belong in the order Ranunculales. The close agreement of the pollen in the four species examined, *Coriaria japonica* A. Gray, *C. myrtifolia* L., *C. ruscifolia* L. and *C. thymifolia* Willd. would remove any doubt about their natural relationship: the grains are suboblate, spheroidal, sometimes angulaperturate in shape; the apertures are 3(–4) pores or very short colpi, sometimes with a thickened margin, placed on the presumed equator; the tectum coarsely granular. The only species examined in thin section, *C. ruscifolia,* has typical dicot stratification: a thin but consistent endexine, diminutive columellae connecting an uneven but probably continuous tectum with a thin, uniform foot layer. It is this unit which is thickened abruptly near the apertures that produces the external crassi-marginate characteristic. It is impossible to deal adequately with families such as this or Corynocarpaceae in a review paper except negatively, i.e., the pollen morphology does not support the present placement of the family in the order Ranunculales. Thorne (1976) has placed the Coriariaceae next to the Simarubaceae and Rutaceae, both of which are known to have a diversity of pollen types. Whether the range of variation would include the one described above remains unanswered.

[Additional pollen samples have been obtained, but not yet examined, for both families. We intend to explore the relationships of the Corynocarpaceae and of the Coriariaceae as suggested by Thorne (1976), and will treat each family in a separate publication.]

LARDIZABALACEAE

The Lardizabalaceae have an unusual distribution, southeast Asia from Nepal to Japan, and Chile. The pollen of 14 species representing 7 genera was examined: *Akebia, Boquila, Decaisnea, Holboellia, Lardizabala, Parvatia,* and *Stauntonia.* With the possible exception of *Stauntonia hexaphylla,* all taxa had 3-colpate aperture types. In *Akebia, Boquila,* and *Holboellia* the colpi are wide and do not taper at the poles. In most taxa the tectum is complete except for punctae of varying size and distribution. A general similarity also exists in thin section: a well-developed endexine, thin foot layer, diminutive, uniform columellae, and a tectum that is the most conspicuous of the ektexine units.

DILLENIACEAE

The investigation of the Dilleniaceae was prompted by the transfer of *Paeonia* from the Ranunculaceae to the order Dilleniales and its elevation to family status,

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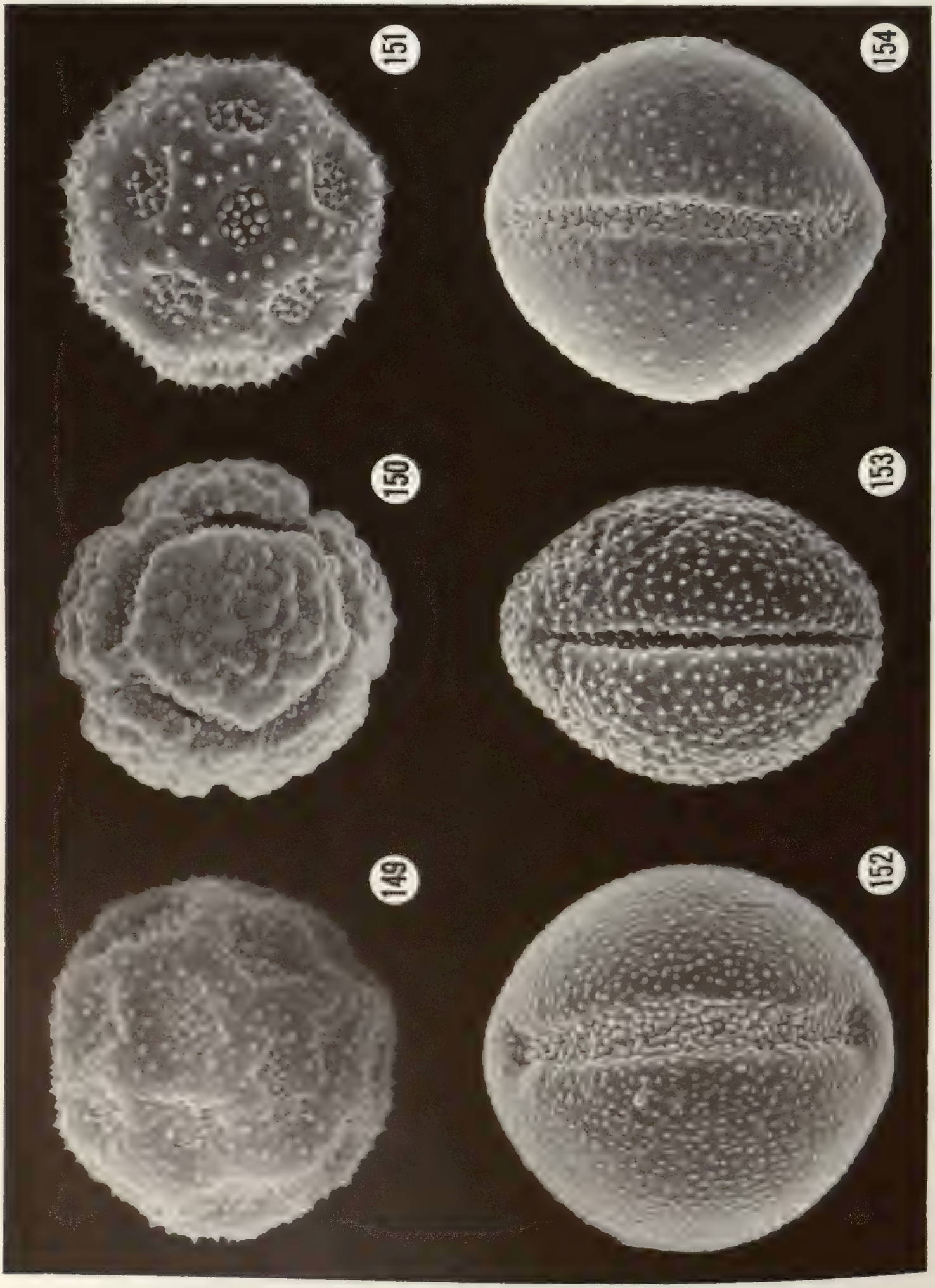
FIGURES 144–148. Transmission Electron Micrographs of Berberidaceae pollen.—144. *Berberis fendleri* A. Gray, ×25,350.—145. *Mahonia nervosa* (Pursh) Nutt., ×11,310.—146. *Podophyllum peltatum* L., ×12,880.—147. *Jeffersonia diphylla* (L.) Pers., ×4,200.—148. *Diphylleia sinensis* Li, ×7,380.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Paeoniaceae. The pollen of approximately 40 species was examined in LM and in SEM, and the following comments are based on this restricted number and technique. Variation within a species and within a sample suggests that pollen morphology will have limited value. There are some species of *Curatella*, of *Davilla* and of *Doliocarpus* that have pollen similar to some species of *Paeonia*: grains which are prolate, 3-colporate (colporoidate), and an incomplete tectum in which the perforations are smaller nearer to the colpi. This type of morphology is a common one in the dicots, and illustrated in this paper by Fig. 129, *Naumbergia thyrsiflora* (Primulaceae) and in *Lysimachia terrestris* (Nowicke & Skvarla, 1977: fig. 177). Some species of *Paeonia* have a pollen morphology similar to that of *Lysimachia hybrida* (Nowicke & Skvarla, 1977: fig. 175) including the bridge of ektexine across the colpus. The type of tectum in *Paeonia brownii*, Fig. 160, in which the perforations are more uniform in size, was not found in the taxa examined of Dilleniaceae. *Actinidia* and allied genera, *Clematoclethra* and *Saurauia*, sometimes recognized as a separate family, Actinidiaceae, are more closely related to each other than to any remaining members of Dilleniaceae. This distinction, a continuous or complete tectum, is not very great, and if additional species of Dilleniaceae s.l. are examined, it may well be lost.

The Dilleniaceae pollen will be examined in thin section and information from exine structure may clarify some of the above relationships.

Adaptive Significance

In a review article which spans such a large number of taxa, the great range of variation in the surface of the tectum, and to a lesser extent in the aperture types and exine structures, raises the fundamental question of the adaptive significance of the variation. There are some correlations between the function of the pollen grain, which is to transfer the male gametophyte and to insure germination, and certain characteristics of the exine.

Protection from desiccation during transfer is basic and the architecture of the wall could logically be interpreted as an adaptation to minimize the effects of water loss: the two concentric spheres (or other shapes), i.e., the foot layer and tectum, whose spatial separation is maintained by the columellae, provides maximum support and rigidity. Adaptations for germination are more conspicuous: preformed breaks in the exine expedite the release of the nuclei; more than one potential exit would permit rapid germination no matter what area of the grain might be in contact with the stigma. A function has been attached to the chamber between the foot layer and tectum: storage of recognition substances that initiate the process of germination. The apertures also function as harmomegathic mechanisms (Wodehouse, 1935; Payne, 1972).

The great diversity in the surface of the tectum is another matter altogether. In Heslop-Harrison's view (1971: 8): "Evidently if we are not to assume that pollen wall sculpturings are no more than meaningless manifestations of a kind

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Figures 149–154. Scanning Electron Micrographs of Ranunculaceae pollen.—149. *Anemone coronaria* L., ×1,780.—150. *Ranunculus muricatus* L., ×1,240.—151. *Coptis occidentalis* (Nutt.) T. & G., ×2,270.—152. *Clematis orientalis* L., equatorial view, ×2,530.—153. *Adonis pyrenaica* DC., equatorial view, ×1,780.—154. *Eranthis hyemalis* (L.) Salisb., equatorial view, ×1,560.

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of morphogenetic virtuosity, we must accept that there is a high adaptive component, and that diversity has resulted from selective forces.'' But has all of the diversity been the result of selective forces?

Of all possible structure-function correlations in pollen morphology, that of pollen-pollination vector has probably attracted the most attention and produced the least consistent results.

Leuenberger (1976: 203), after examination of 600 species in the Cactaceae, reported that ''The data obtained so far do not support the assumption that clear correlations exist between exine sculpturing and pollination types.''

Taylor & Levin (1975) reported similar and wider conclusions in the Polemoniaceae. In their discussion they note that (p. 104) ''it is appropriate to question at this point whether different exine organization patterns reflect adaptations to different pollen dispersal mechanisms. The data presented here do not substantiate such a relationship.'' Nor did they find a relationship between pollen ornamentation and environmental parameters. And, while conceding that features of wall configuration might prove to be correlated with some parameters, Taylor and Levin considered the adaptive significance of the various patterns to be a matter of conjecture. (It should be added that none of the Polemoniaceae are known to be wind pollinated.)

However critical may be the need to control desiccation in wind-pollinated grains, the priority appears to be buoyancy. In this transfer method each individual grain has the entire surface exposed to climatic stress. Most animal-pollinated grains have a pollenkitt, an oily-waxy coating that prevents or reduces evaporation from the surface of the grain. The pollenkitt also causes the grains to clump together, and during transfer those grains in the interior of these sticky masses are protected from physical damage as well. Wind-pollinated grains lack, apparently, adaptations which would reduce water loss. The same coating which would reduce evaporation would probably cause the grains to clump with loss of buoyancy; a thicker exine, which might withstand early collapse due to the shrinking volume of protoplasm, would add weight and loss of buoyancy. In fact, even the size of these grains is disadvantageous in preventing desiccation. The volume of a sphere increases with the cube of the radius while the surface increases with the square of the radius; thus smaller grains present more surface area per unit volume than larger spheres. Admittedly in the wind-pollinated Gramineae, characteristics of the aperture, one crassimarginate pore with an aperture plate, could logically be interpreted as adaptations to reduce desiccation.

On the other hand, the predominantly wind-pollinated Amaranthaceae and Chenopodiaceae have grains with numerous small pores, e.g., Fig. 9, fewer but larger pores, e.g., Figs. 28 and 34, or larger and recessed pores, e.g., Figs. 29–30, 35–36. Structural modifications that provide additional support, such as a thick tectum, e.g., Figs. 41–42, and 48, and/or robust columellae, e.g., Fig. 48, may function to counteract the desiccating properties of the apertures, but not without a loss of buoyancy.

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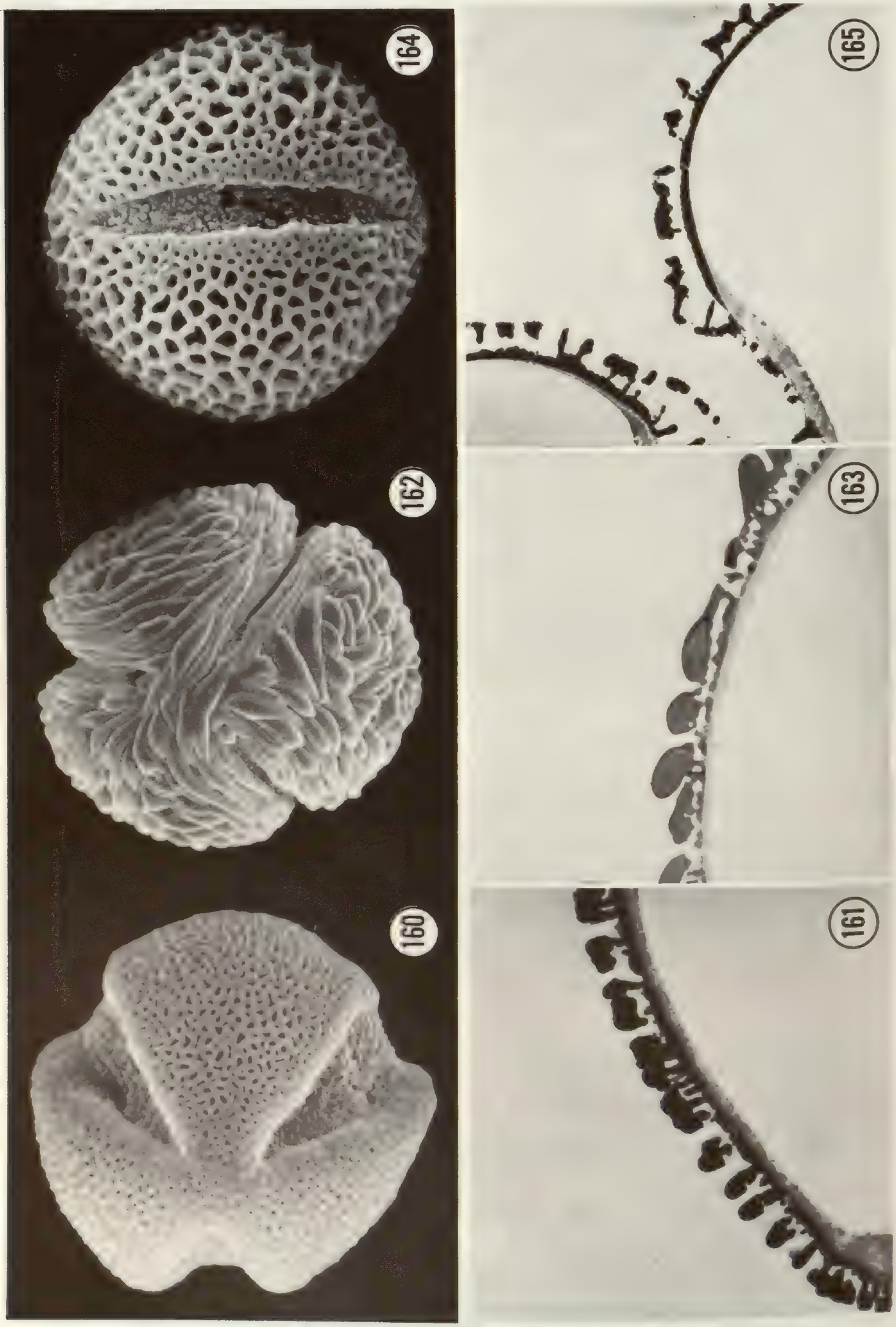
FIGURES 155–159. Transmission Electron Micrographs of Ranunculaceae pollen.—155. *Anemone coronaria* L., ×4,200.—156. *Clematis orientalis* L., ×7,540.—157. *Ranunculus muricatus* L., ×5,040.—158. *Adonis pyrenaica* DC., ×11,730.—159. *Coptis occidentalis* (Nutt.) T. & G., ×11,020.


164
162
160
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161

It may well be that cryptic mechanisms residing in the cytoplasm function to reduce water loss, perhaps in the same manner that permits halophytes to absorb water against the gradient, but this is active absorption and expends energy.

The adaptive significance of the tectum diversity has become more obscure with an increasing number of results or observations which appear contradictory. In particular, there are two somewhat paradoxical phenomena that are difficult to reconcile in a limited framework of structure/function. On the one hand, quite diverse tecta or even pollen morphologies occur within the same genera, while, on the other hand, the same or very similar, specialized tecta and sometimes pollen morphologies occur in unrelated genera of widely separated families.

The first phenomenon is well known and there are numerous examples. Three examples from our own studies can be cited. The large genus *Tournefortia* has four pollen types, one of which, III, is remarkably distinct (Nowicke & Skvarla, 1974). In vegetative and floral morphology *Podophyllum emodi* and *P. peltatum* are obviously closely related, but palynologically they are widely separated (Nowicke & Skvarla, 1979). *Polygonum* s.l. may have the greatest pollen diversity in the angiosperms (Hedberg, 1947; Nowicke & Skvarla, 1977).

The second phenomenon depends upon the demonstration or proof of pollen similarity, and for the most part the discovery of very similar pollen in widely separated families is the direct result of a technological advancement, the scanning electron microscope. The examples may not be as numerous as in the first case, but it is only a matter of time.

The pollen morphology found in *Tournefortia angustifolia* and related species, Type II (Nowicke & Skvarla, 1974: figs. 10–18), is very similar to that of some members of *Sonneratia* (Muller, 1969: plate IV, fig. 5, plate XI, figs. 1–2).

Phyllanthus casticum in the Euphorbiaceae (Bor, 1979: plate VIII, fig. 5), admittedly a member of a eurypalynous genus, is nonetheless very similar to *Schisandra grandiflora* in the Schizandraceae (Walker, 1974: fig. 42), and these families are not considered to be related.

Simmondsia, a monotypic genus found in the warm arid regions of North America, is one of the dicot taxa of uncertain affinities. The tectum is (almost?) identical (Nowicke & Skvarla, unpublished data) to that found in *Valeriana palmeri* (Clarke, 1978: fig. 12), although the aperture condition, three poorly defined pores, is not.

If palynologists and systematists accept the view that pollen variation has a high adaptive component, then all of the above examples, either the diversity of pollen in closely related species, or the similarity of pollen in widely separated taxa, can be attributed only to selective forces.

Although Taylor & Levin (1975) avoid the use of selective forces, the following quotation from their Phylogenetic Interpretations is of considerable interest (pp. 110–111): "Scanning electron microscopy may prove to be a very valuable tool

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FIGURES 160–165. Scanning Electron Micrographs and Transmission Electron Micrographs of Ranunculaceae pollen.—160. *Paeonia brownii* Dougl., SEM, slightly oblique polar view, ×1,990.—161. *P. brownii*, TEM, ×6,350.—162. *Trollius acaulis* Lindl., SEM, polar view, ×2,370.—163. *T. acaulis*, TEM, ×6,350.—164. *Helleborus viridis* L., SEM, equatorial view, ×1,920.—165. *H. viridis*, TEM, ×1,020.

in elucidating species relationships within the Polemoniaceae, especially if pollen morphology is largely free from the confronting elements of parallel evolution. This rule of thumb may be applied to the pollen morphology of the Polemoniaceae, although with due caution. Implicit in our argument is the proposition that congruity in wall architecture is not the product of parallel evolution, but is the manifestation of long-standing structural similarity dictated by common ancestry. We fail to identify any environmental conditions, biotic or abiotic, which may account for parallel evolution. The adaptive radiation in pollen morphology leading to major 'pollen lineages' ostensibly was initiated and nearly completed long ago, in contrast to more recent differentiation within genera for other aspects of their pollination biology.''

The lack of success in identifying environmental conditions and/or selective forces, either on the part of Taylor & Levin (1975) or us, does not deny their existence, but data from studies such as those on the Polemoniaceae and the Cactaceae (Leuenberger, 1976) and the discovery of similar pollen in widely separated taxa could be interpreted as evidence that some pollen variation stems from relictual adaptations. The most plausible explanation of the close similarity of specialized pollen morphologies in the Caryophyllaceae and the Amaranthaceae would be common ancestry. But if the adaptive significance of pollen characteristics is obscure in the present, it is unlikely to be clarified in the past.

SUMMARY AND CONCLUSIONS

Within the angiosperms there are an estimated 300 families whose segregation into orders is based on the same premise as all the preceeding and lower ranks: these particular families (genera, species, etc.) are thought to be more closely related to each other than to any remaining ones. But the distinction between family and order is of much greater magnitude than between genera and families. The characteristics that define orders are frequently so generalized that their presence in a group of families is as likely to indicate parallel or convergent evolution as it is relationship and/or a monophyletic origin. Many of the larger orders are thought to be artificial, and it is not uncommon to find a family ''doubtfully referred to . . .'' or ''largely for convenience . . . .''

The above reservations do not apply to the Centrospermae, and with at least 13 families and 10,000–12,000 species, it is the best example of a large, natural order in the dicotyledons. These families are united by a series of embryological characteristics which would satisfy the most ardent splitter, but two unique variations, one chemical, the betalains, the other cellular, protein sieve-tube plastid, are responsible for the order's great prominence in systematic research of the last decade.

Pollen morphology, more specifically the presence of a spinulose and punctate/perforate tectum in the vast majority of the taxa examined in the Centrospermae (Table 2), reinforces the close relationship accorded these families from other sources (Table 2). We would include these families in the Centrospermae: Achatocarpaceae, Aizoaceae, Amaranthaceae, Basellaceae, Cactaceae, Caryophyllaceae (including *Geocarpon*?), Chenopodiaceae (including *Dysphania*), Didiereaceae, Halophytaceae, Molluginaceae, Nyctaginaceae, Phytolaccaceae (including *Stegnosperma*), and Portulacaceae (including *Hectorella* and *Lyallia*?).

TABLE 2. Summary of results of pollen analysis.

	Taxa Examined	Ektexine	
	Species/Genera	Spin. + Tub./Punct.	"Other"[a]
Plumbaginaceae (10–15)	20/9	0	20
Polygonaceae (40)	100/40	4	96
Primulaceae (28)	29/22	0	29
Betalain Families plus Caryophyllaceae and Molluginaceae	238	205	33
Ranunculaceae	134/42	111	23
Berberidaceae	39/13	0	39
Lardizabalaceae	14/9	0	14
Dilleniaceae	41/13	0	41

[a] Any tectum other than spinulose/punctate.

The Amaranthaceae and the Chenopodiaceae are more closely related palynologically to certain separate factions in the Caryophyllaceae than they are to each other. The caryophyllaceous genus *Siphonychia* and the amaranthaceous genera *Alternanthera*, *Gomphrena*, *Iresine*, *Pfaffia*, and *Tidestromia* have a very similar and very specialized pollen morphology which is not known to occur in the Chenopodiaceae. The chenopodiaceous genera *Anabasis*, *Halocharis*, *Nitrophila*, and *Traganum* have a pollen morphology that is more closely related to the caryophyllaceous genera *Cerastium*, *Drypis*, *Gymnocarpos*, *Paronychia*, and *Scleranthus* than to any members of the Amaranthaceae.

The pollen morphology of *Achatocarpus* and *Phaulothamnus* is distinct from all other Centrospermae, but the presence of betalains and the protein type sieve-tube plastid are irrefutable evidence that they do belong to this order. Their affinities within the Centrospermae and the level of recognition remain unanswered.

In each of three small families the pollen morphology is sufficiently distinct to be the key characteristic in establishing their relationships and position in the dicot hierarchy: the unstratified exine in Batidaceae; the unique (?) exine structure in Gyrostemonaceae; the zonoporate apertures and false reticulum tectum in Theligonaceae. We do not believe that the Batidaceae and Gyrostemonaceae are closely related, palynologically or otherwise; nor do we believe that the genus *Theligonum* is closely related to the Rubiaceae.

The pollen morphology of the Plumbaginaceae, Polygonaceae, and Primulaceae does not support a close relationship of any of these families to the Centrospermae nor to each other. Nevertheless, some of the results from the investigations of the first two families deserve mention: the Plumbaginaceae have only two pollen types, Armeria and Plumbago, which are remarkably distinct from each other in the structure of the exine and in the exomorphology; the Polygonaceae have great diversity in pollen types due to variation in all characteristics, apertures, surface sculpture, and the structure of the exine.

The preliminary investigation of the order Ranunculales indicates that the families Ranunculaceae, Berberidaceae, Lardizabalaceae, Coriariaceae, and Corynocarpaceae are not closely related on the basis of pollen morphology.

The Ranunculaceae have very uniform pollen with a spinulose and punctate/perforate tectum which closely resembles that found in the Centrospermae. The only taxa which do not have this tectum are *Helleborus*, *Hydrastis*, *Paeonia*, and *Trollius*.

The pollen morphology of the Berberidaceae s.l. is much more diverse and supports in part the concept of the family as closely related groups of genera. The very primitive pollen found in *Berberis* and *Mahonia* reinforces their treatment as a separate family. *Nandina* has distinctive pollen which could be used to support separate family status. Most of the remaining genera have a pollen morphology similar to various species in the Old World genus *Epimedium*, and, while all are not equally or closely related, it is a more natural grouping than previously thought. The pollen of *Diphylleia* and especially of *Podophyllum emodi* is distinct in the Berberidaceae s.l., and from all other taxa examined in the framework of these studies.

Although the pollen morphology of Coriariaceae does not have the diagnostic features found in some of the other small families, it could provide the most efficient means to evaluate the suggested relationship to the Simarubaceae. We do not believe that Coriariaceae belongs to the order Ranunculales.

For Corynocarpaceae the unusual characteristics of the pollen, especially the poorly differentiated structure of the exine, eliminate any close tie to the Ranunculales but do offer great potential as key characteristics.

For the most part the pollen of the Dilleniaceae appears to have limited value as a taxonomic parameter due to the wide and overlapping variation found in the larger genera, *Dillenia*, *Hibbertia*, *Tetracera*, etc. The close relationship attributed to *Actinidia*, *Clematoclethra*, and *Saurauia* on other bases is supported by their pollen morphology, but the distinction is not very great.

The pollen morphology of the Lardizabalaceae is relatively uniform and unspecialized and does support the present concept of the family.

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ONTOGENY OF EXINELESS POLLEN IN *HELICONIA*, A BANANA RELATIVE[1]

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ABSTRACT

The pollen of *Heliconia* and most of its zingiberaceous relatives is destroyed by the standard acetolysis preparation. The fragility of the grains is the result of the weak exine development and sporopollenin deposition. There is a corresponding enhancement of intine growth. Transmission electron microscope studies were conducted on the pollen ontogeny from the microspore mother cell stage to the mature microspore in order to determine the nature of sporoderm development and differentiation. Ontogeny of the *Heliconia* sporoderm is similar to the basic pattern of angiosperm pollen development through the tetrad stage. The primexine template is established while the callose sheath still envelopes the tetrad microspores. Probacula arise from the plasmalemma of each microspore but only on the distal hemisphere in *Heliconia*, and then white lines develop between the plasmalemma and the probacula bases. Limited amounts of protosporopollenin from the microspore protoplast are deposited on and around the white lines. Dissolution of the callose brings tapetal lipid globules into contact with the developing exine, and there is some evidence that tapetal membrane fragments become attached to the primexine template. For the most part, however, sporopollenin deposition is minimal during the free spore stage in *Heliconia*. The consequence is that the exine consists of probacula which mature into spinules and white lines which are coated with thin deposits of sporopollenin to form stratified lamellae. As in other pollen, the intine of *Heliconia* is initiated during the free spore period following microspore enlargement and the formation of a large central vacuole. Microfibrils of cellulose develop between the plasmalemma and mature exine. The outermost fibrils are compacted and the radially oriented vesicles which appear in the intine region apparently are active in dissolving channels through to the base of the exine. Additional fibrils are eventually deposited to the interior of the intine to seal off the channels. Channel formation in *Heliconia* proceeds rapidly and is restricted to the distal hemisphere, while development of the proximal face is somewhat retarded and the mature intine is solid and stratified. The functional significance is not known, though the channels could serve as reservoirs for gametophytic proteins involved in germination and incompatibility.

Systematic botany has come to rely on the acetolyzed remains (viz. exine) of pollen and spores for routine identifications and speculations on angiosperm phylogeny. From a functional point of view, of course, the exine which has undergone acetolysis treatment is a skeleton devoid of the vital signs that make the mature pollen grain a precarious biological bridge between sporophytic generations.

Questions about the functional, adaptive, or evolutionary significance of pollen must consider the total life history of a pollen grain and be aware of the limitations imposed by the study techniques. The genus *Heliconia* and some of its zingiberaceous relatives are a case in point. The grains are large and have a relatively thick sporoderm. They are readily destroyed, however, in the standard acetolysis solution. The reason for this fragility is that the exine which normally forms a tough outer coat impregnated with acid resistant sporopollenin is either very thin, discontinuous, or absent in the Cannaceae (Skvarla & Rowley, 1970), Heliconiaceae (Kress et al., 1978), Lowiaceae, Marantaceae, Musaceae, Strelitziaceae, and Zingiberaceae (Heslop-Harrison, 1976; Stone et al., unpublished).

The significance of a virtually exineless pollen grain in most of the Zingiberales (sensu Tomlinson, 1962) is not known. Reports of other monocotyledons with a

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thin pollen exine and very thick intine, often striated with radially oriented channels, include members of the ancestral Liliales (i.e., Amaryllidaceae, Iridaceae: Heslop-Harrison, 1976). The apertural regions of the grasslike Restionales and *Degeneria* of the dicotyledons are also reported to have a radially striate intine. These observations led Skvarla & Rowley (1970) to surmise that the "entire pollen wall" of *Canna* (Cannaceae) is, effectively, one large aperture that offers "an infinite number of sites for pollen tube initiation." While the advantages of such a versatile pollen grain are apparent (Lee, 1977, 1978), there is no suggestion as to why the condition is common only to a few monocot allies. Some clues might be gleaned from the anomalous pollen of *Heliconia*. This genus and some members of the Costaceae have heteropolar pollen (Stone et al., unpublished). The radial striations of *Heliconia* seen with brightfield microscopy prove to be densely packed cylindrical channels that are confined to one hemisphere (Kress et al., 1978). Conceivably, this specialized pollen type has some adaptive significance in the reproductive biology of the hummingbird-pollinated *Heliconia* species.

Investigations on the ontogeny of the pollen grain wall of *Heliconia* were initiated to (1) confirm the polarity; (2) determine the developmental pattern of the exine; (3) establish the nature and sequence of development of the highly elaborated intine; and (4) provide a firm basis for investigating the functional role of the grains in pollination biology and the usefulness of mature pollen in assessing the broader phylogenetic relationships within the order.

MATERIALS AND METHODS

In preparation for acetolysis and scanning electron microscopy (SEM), mature, unopened flowers were collected from plants in the field or greenhouse (Table 1) and fixed in formalin-acetic acid-alcohol (FAA) for at least 24 hours. The anthers were then dissected from the flowers, taken through the standard acetolysis preparation (Erdtman, 1969) and mounted in glycerine jelly for observation with phase microscopy (Leitz Ortholux with Heine condenser). Since acetolysis proved devastating to the delicate *Heliconia* pollen grains, critical point drying was employed to reduce surface tension distortion of the sporoderm (Lynch & Webster, 1975). The anthers were dissected from the flowers after fixation, transferred to 70% ethanol, and then dehydrated through a series of steps ending in 100% Freon. The critical point drying was carried out in a BOMAR SPC 900/EX dryer with CO_2 as the transitional fluid. The anthers were opened and the dried pollen shaken out onto a glass coverslip overlaid by a thin film of polyvinyl chloride adhesive (Leffingwell & Hodgkin, 1971). The pollen was shadowed with approximately 200 Å of gold-palladium and viewed with a JEOL JSM-S1 SEM.

Transmission electron microscope (TEM) observations were conducted on plants from the greenhouse. Entire flowering bracts were harvested and the individual flowers subtended by each bract were sequenced and labeled according to size. The anthers were dissected from each flower and fixed. In the preliminary studies FAA fixation was tried but disruption of the cytoplasm obscured internal detail. Critical ontogenetic studies depended on routine fixation with 4.2% glutaraldehyde (diluted from 70% stock) in a 0.1 M Sørensen's phosphate buffer at pH 7 for 1 hour at 20°C. After 5 washes in phosphate buffer, the anthers were

TABLE 1. *Heliconia* collections examined.

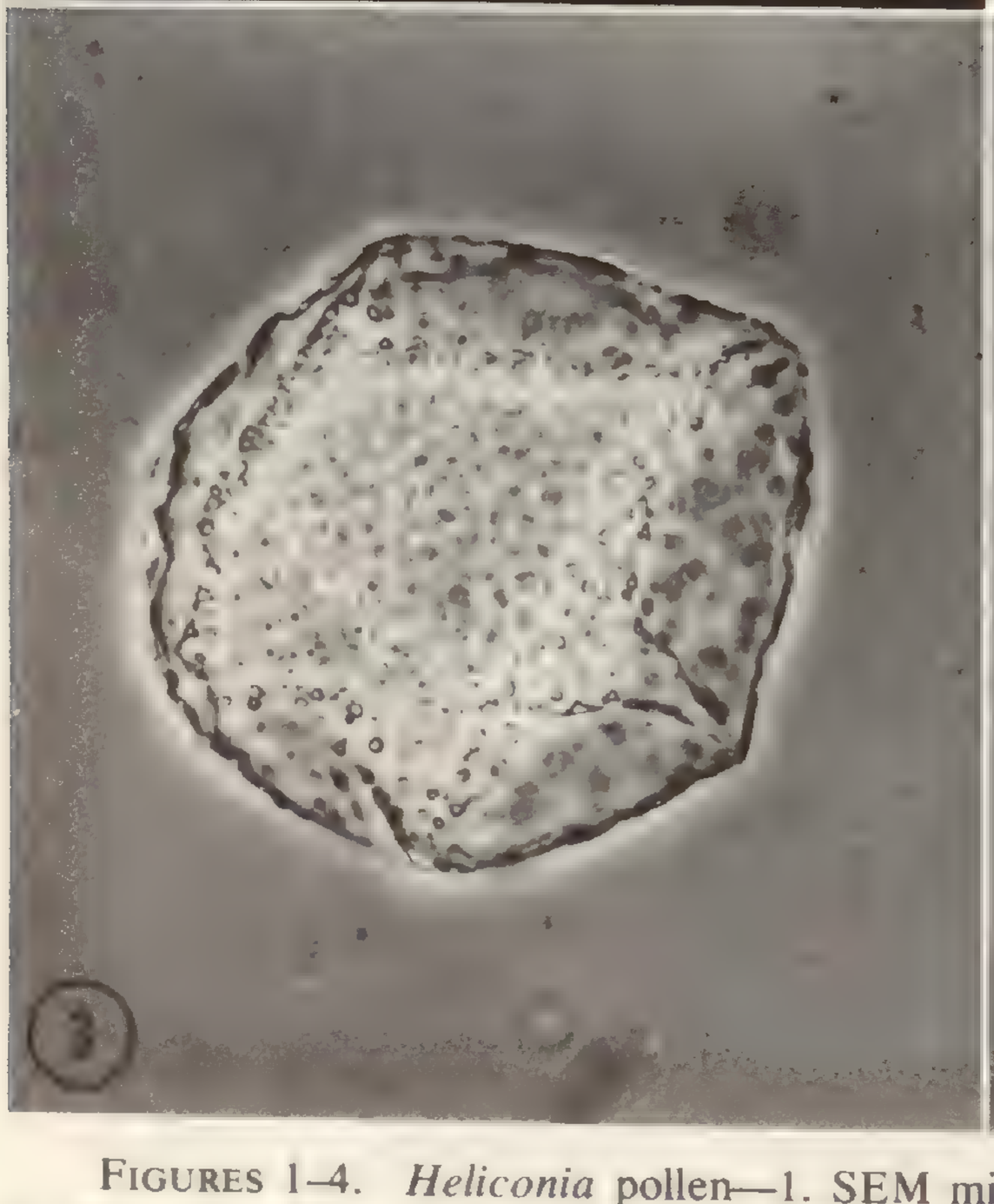
Species	Collection Data
H. irrasa R. R. Smith var. *irrasa*	COSTA RICA. PUNTARENAS: Esquinas Forest Reserve between Río Claro and Palmar, 75 m, July 1976, *Kress, Cooper-Smith, Daniels, Stiles & Hutchison 76-591* (DUKE).
H. nutans Woodson	PANAMA. CHIRIQUÍ: 5 mi from Boquete near Finca Lerida, 1,700–1,800 m, Aug. 1977, *Kress, Clarkson & McDade 77-882*. Rhizomes imported and plants raised to flowering at Duke Univ. (DUKE).
H. "Peru" (*cf. brasiliensis* Hook.)	PERU. JUNÍN: Along road between Tarma and San Ramón, 2,300 m, Feb. 1976, *Kennedy & Plowman 3564*. Seeds germinated and plants raised to flowering at Duke Univ. (DUKE).
H. "Ecuador" (sp. nov.; aff. *humilis* Jacq.)	ECUADOR. PASTAZA: Mera, Nov. 1974, *Plowman 7609*, live collection only. Rhizomes sent to Kress (*79-1052*) and plants raised to flowering at Duke Univ. (DUKE).

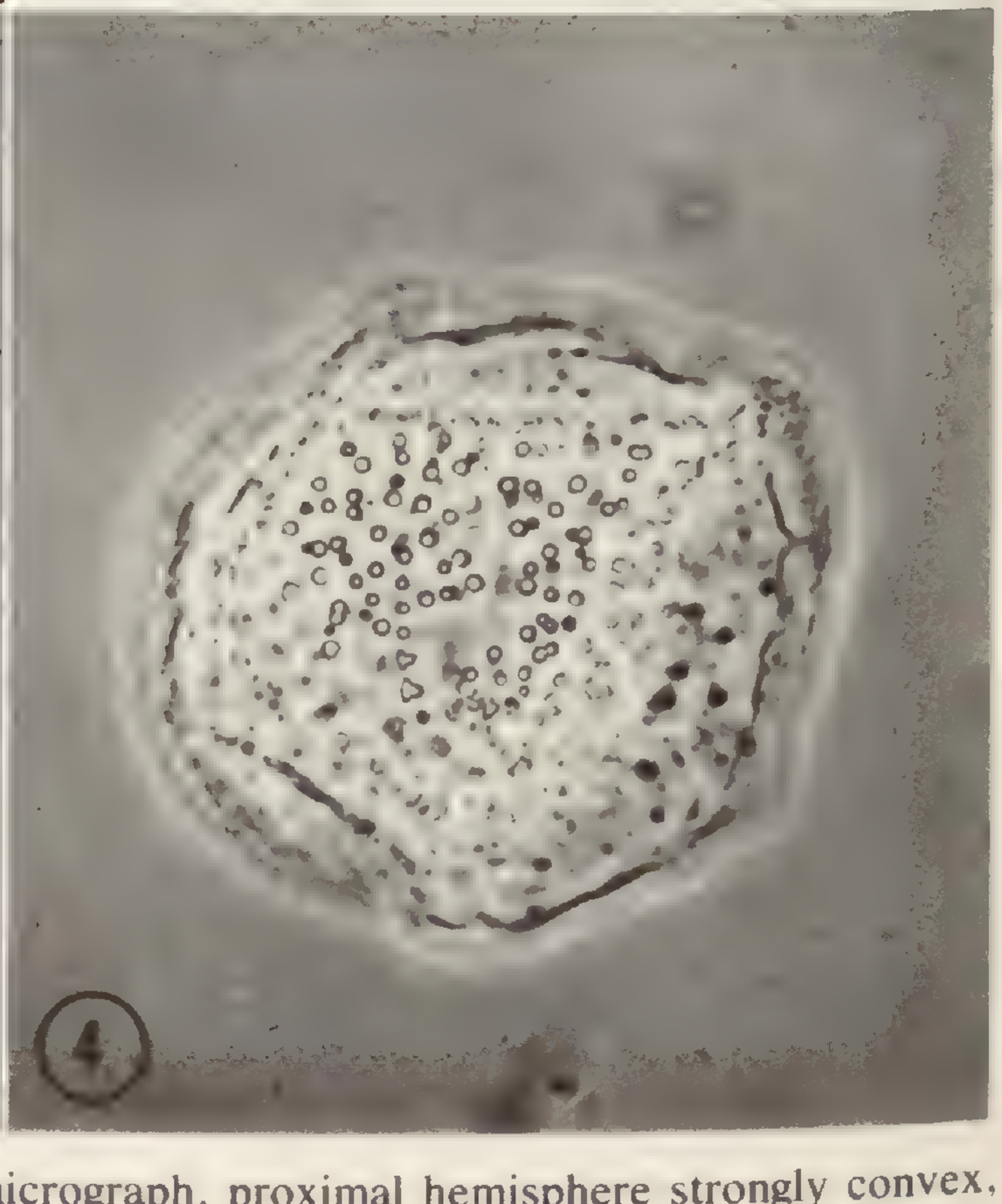
post-fixed for 1 hour at 20°C in 2% OsO_4 in 0.1 M phosphate buffer. The material was again rinsed in buffer, dehydrated, and then infiltrated with epoxy resin (Spurr, 1969). The entire procedure from fixation through infiltration was carried out under vacuum. Sections were cut on a Cambridge-Huxley ultramicrotome with a DuPont diamond knife. Ultrathin sections were post-stained with saturated uranyl acetate in 50% ethanol followed by 0.2% lead citrate. Photomicrographs were taken on a Siemens Elmiskop 101 TEM. Thick sections (0.5–1 μm) for viewing with brightfield microscopy were stained in a drop of toluidine blue dissolved in 1% aqueous solution of borax (Pease, 1960). Permount was used as the mounting medium for permanent slides of the pollen sections.

Unfortunately, only limited analyses have been accomplished to confirm the specific nature of the wall components in *Heliconia*. Our use of such terms as callose, cellulose microfibrils, sporopollenin, etc. is based mainly on similarities in ultrastructure with published reports of pollen grains that have been examined by histochemical procedures.

RESULTS

Mature pollen of *Heliconia* is large (to 80 μm or so) and inaperturate (Fig. 1). The unique nature of the grain is not readily apparent, however, because the sporoderm is exceptionally thick (to 8 μm) and rigid enough to withstand transport in pollination (Fig. 2). The relatively fragile construction of *Heliconia* pollen is revealed by applying mild acetolysis treatment. The proximal hemisphere which seems to be more resistant to the treatment maintains its integrity for a while as a thin shell (Fig. 3), whereas the striated distal hemisphere collapses into the hollowed interior of the grain (Fig. 4). In a previous study we determined that sporoderm thickness is due to a massive and complex intine (Kress et al., 1978: see fig. 14). The exine is limited to discontinuous patches of spinules on the distal surface and a thin corrugated layer on the proximal hemisphere, no doubt accounting for the short-lived pollen shell in acetolysis. The initiation and development of pollen was followed in the anther from the archesporial stage through





FIGURES 1–4. *Heliconia* pollen—1. SEM micrograph, proximal hemisphere strongly convex, *H.* "Peru," ×830.—2. Brightfield micrograph of "thick" section, equatorial view, minute spinules and channels on distal face, hemispheres approximately equal in size, *H.* "Peru," ×870.—3. Phase contrast micrograph of an acetolyzed grain viewed from distal pole: fragile channelled surface collapsed into grain with upright edges of proximal hemisphere forming shell, *H. irrasa*, ×555.—4. As above, focal plane near bottom of grain showing surface spinules of collapsed distal "roof," *H. irrasa*, ×555.

meiosis to the maturation of a mature male gametophyte, with particular emphasis on the nature and ontogeny of the sporoderm (Fig. 5).

PRE-TETRAD PERIOD

Prior to meiosis any one plane of the anther locule contains a relatively few (up to 9), large sporogenous cells surrounded by a single layer of tapetal

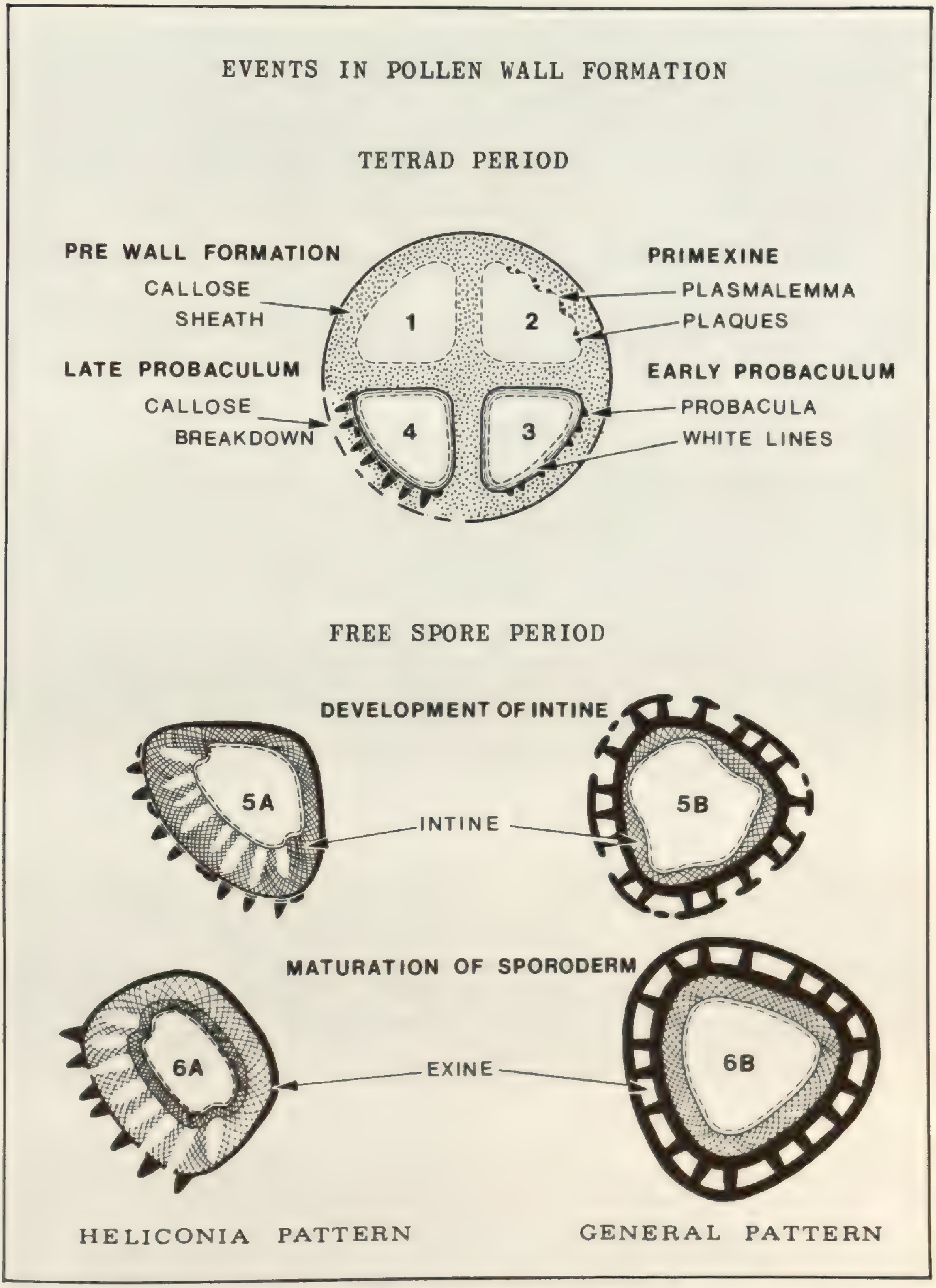


FIGURE 5. Ontogenetic development of pollen wall formation in *Heliconia* and the general pattern in grains with well-developed exines.

cells (Fig. 6). Adjacent sporogenous cells have numerous protoplasmic connections through plasmodesmata (Fig. 7), thus affording communication between the sporogenous mass and some degree of synchrony in development. Tapetal cell walls are lost at the termination of meiosis and lens-shaped bodies (LSBs) are discharged into the canals between adjacent tapetal protoplasts (Fig. 8).

TETRAD PERIOD

Pre-wall Formation.—Following meiosis the plasmodial-type tapetal cells show elaborate organelle development and LSBs aggregated on the periphery of the callose sheath (Fig. 8). The four microspores are separated by callose and bound in a tetrad by the special callose wall (Fig. 9). While the callose is continuous and unperforated between microspores, cytomictic channels are in evidence in the callose wall surrounding the tetrad of some species (e.g., Fig. 10, *H.* "Peru").

Primexine Plaque.—Localized invaginations of the plasmalemma form pockets on the distal hemisphere. A fibrous layer and electron dense plaques are deposited to the exterior of the membrane (Fig. 11).

Probaculum.—The growth of the plaques is not understood, but it appears that they enlarge by the acquisition of protosporopollenin from the microspores to become prominent probacula that intrude into the closely appressed callose wall (Fig. 12). By the mid-probaculum stage (Fig. 13) the primexine forms a continuous electron dense band around each microspore protoplast and the nascent spinules reach maturity.

A closer look (Fig. 15) reveals that development of the primexine consists of heavy protosporopollenin concentrations at probacula sites and more diffuse deposits along the tangentially oriented white lines. In the case of multiple white lines (Fig. 16), the outermost (two?) lines concentrate the bulk of the protosporopollenin at a time when the callose wall is still serving as a barrier to tapetal contact. The late-probaculum stage is marked by the partial dissolution of the callose wall that surrounds the tetrad and separates each microspore (Fig. 14). The smooth primexine on the proximal hemisphere shows some thickening between the mid- and late-probaculum stage. Four to six ribbonlike white lines are in evidence to the exterior of the plasmalemma (Fig. 16). The white lines occasionally pass through the central region of the spinules, but more often they are situated near the base (Fig. 17). Localized deposits of protosporopollenin condense on the white lines in template fashion between the spinules (Fig. 18).

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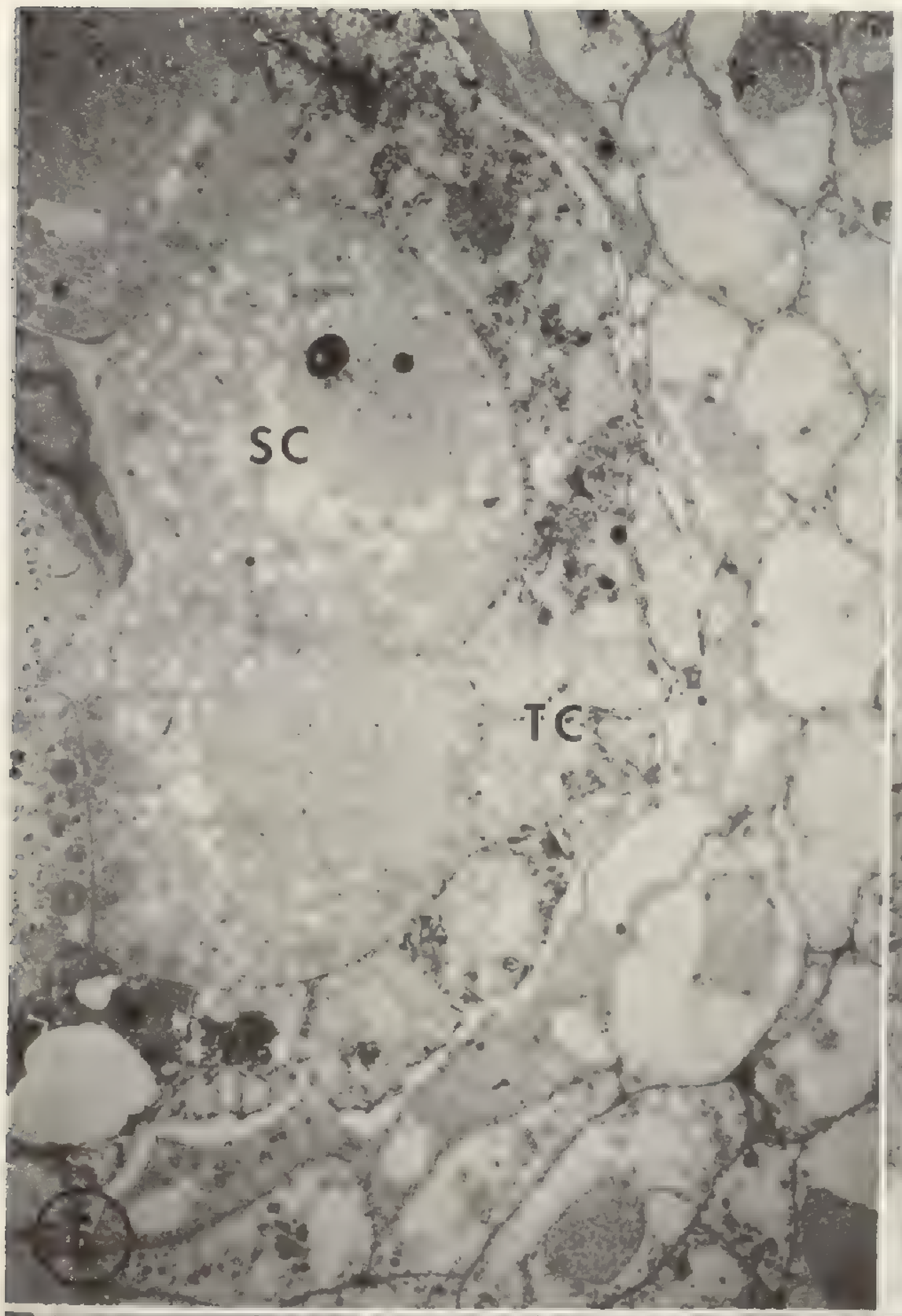
FIGURES 6–10. Pre-meiotic to early tetrad period.—6. Sporogenous cells (SC) with large nuclei and peripheral plastids; adjacent tapetal cells (TC) with relatively undifferentiated protoplasts. *Heliconia nutans*, ×1,250.—7. Plasmodesmata between sporogenous cells, *H. nutans*, ×25,000.—8. Tapetal protoplast (cell wall dissolved) and free LSBs appressed to callose wall (CW) during early tetrad stage, complex protoplast with ribosome packets and scattered vacuoles, *H.* "Brazil," ×12,500.—9. Young tetrad of microspores, cytoplasm disrupted by FAA fixation, *H.* "Peru," ×1,875.—10. Enlargement of peripheral callose wall showing evidence of cytomictic channels (arrows); no channels or pores evident in callose walls separating adjacent mircrospores, *H.* "Peru," ×6,000.


SC
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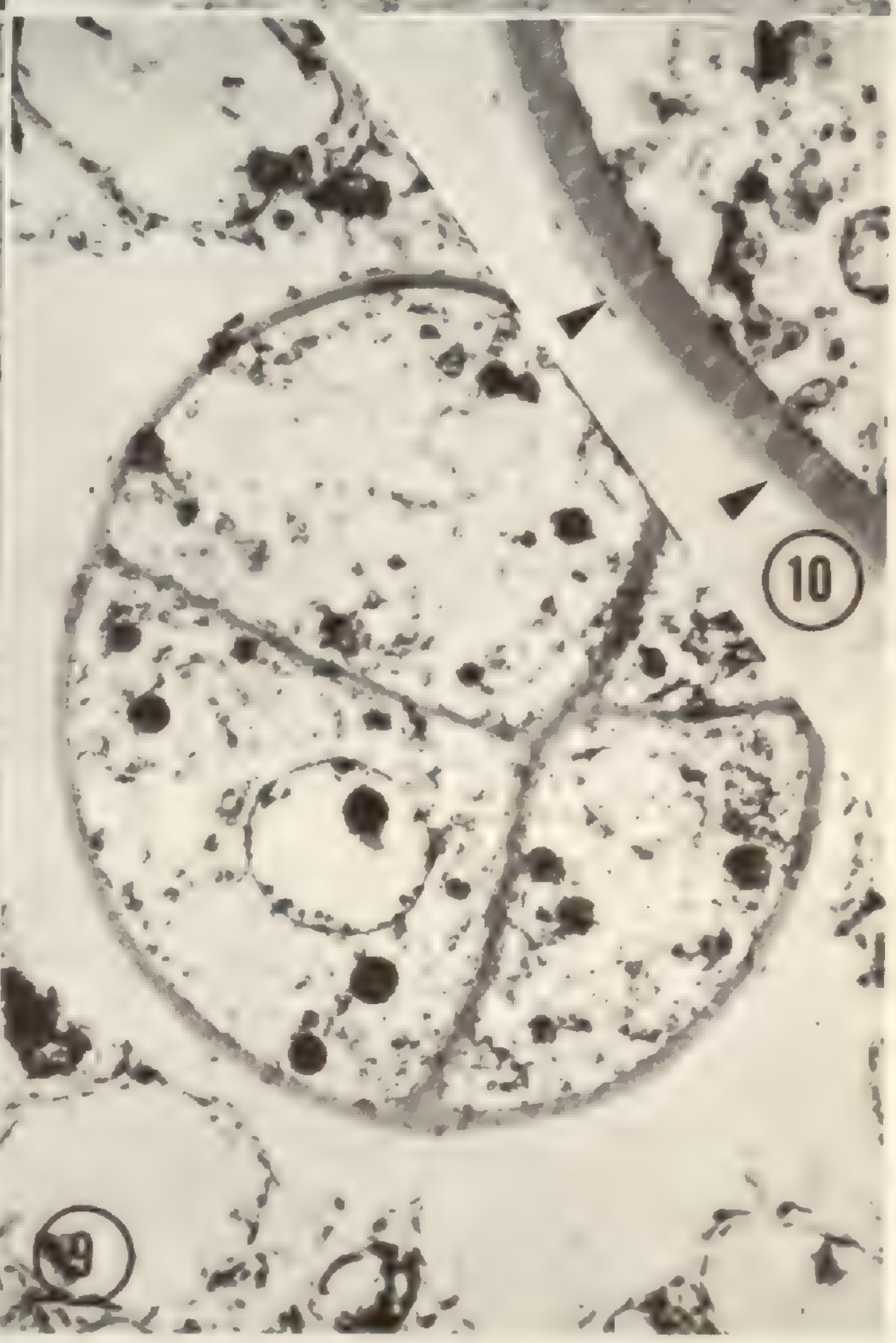
CW



FREE SPORE PERIOD

The complete dissolution of the callose wall which frees the microspores from the tetrad is accompanied by a several fold increase in miscrospore size and the formation of a large central vacuole (Fig. 19). The cytoplasm is compressed against the periphery. In the case of *Heliconia* the majority of the organelles are displaced to the distal hemisphere to form a thicker sheet of cytoplasm than on the proximal side (Fig. 19). At the same time the tapetal protoplasts disintegrate to discharge the contents into the anther locule (Fig. 20).

Initiation of Intine.—The first evidence of intine formation apears as loosely arranged microfibrils situated in pockets between the plasmalemma and the white-line template (Fig. 21). In some cases the fibrillar intine is associated with highly elaborated microspore cytoplasm that shows complex folding of the endoplasmic reticulum (ER) and abundant ribosomes and Golgi apparatus (Fig. 22).

Maturation of Exine.—The exine of *Heliconia* reaches maturity during the early development of the intine. The spinules on the distal face are anchored on the white lines which are mainly tangentially oriented, although occasional views reveal a single radial line passing into the center of a spinule (Fig. 21). The free spore period places the developing sporoderm in contact with the surrounding tapetal discharge (Fig. 23). The LSBs appear to hover around the sporoderm and fragments of tapetal ER with osmiophilic granules (Figs. 23–24) become appressed to the white lines which are of unit membrane dimension (30–40 Å). The formation of a large central vacuole and rapid enlargement of the microspores following release from the tetrad must stretch the sporoderm. This results in separation of the outer white lines (Fig. 27). The surface of the mature grain retains many of the spinules, but the channeled intine is exposed throughout by the sloughing of the poorly anchored exine (Fig. 33).

In summary, initial development of the proximal exine is in phase with that on the distal face. A faint indication of white lines appears between the plaques on the distal surface (Fig. 12), while the proximal surface of the same grain (Fig. 25) shows clear evidence of white lines to the exterior of the plasmalemma and adjacent to the callose wall separating sister microspores. The proximal exine lags behind in development, but by the late tetrad stage it forms a continuous layer that is markedly thicker than the distal exine (e.g., Figs. 36 vs. 33). For all practical purposes one can say that exine formation in *Heliconia* is not enhanced by sporopollenin deposits from the tapetum.

Maturation of Intine.—With the continued elaboration of microfibrils in the undulations to the exteior of the plasmalemma on the distal hemisphere (Fig. 22), tangentially oriented microfibrils become compacted into a thick homogeneous layer beneath the exine, while a loose arrangement of microfibrils occupies an equal space adjacent to the plasmalemma (Fig. 27). The microspore cytoplasm appears particularly active in the areas of microfibril accumulation; plastids and microtubules are abundant and the plasmalemma is diffuse (Fig. 28). The earliest signs of channels in the intine occur after the compacted microfibrils have been layed down beneath the exine (Fig. 27) and at the same time that radially oriented vesicles appear in the fibrillar area adjacent to the plasmalemma (Fig. 29). The diameter of the vesicles corresponds roughly with the width of the nascent channels and our assumption is that the vesicles are active in the dissolution of chan-

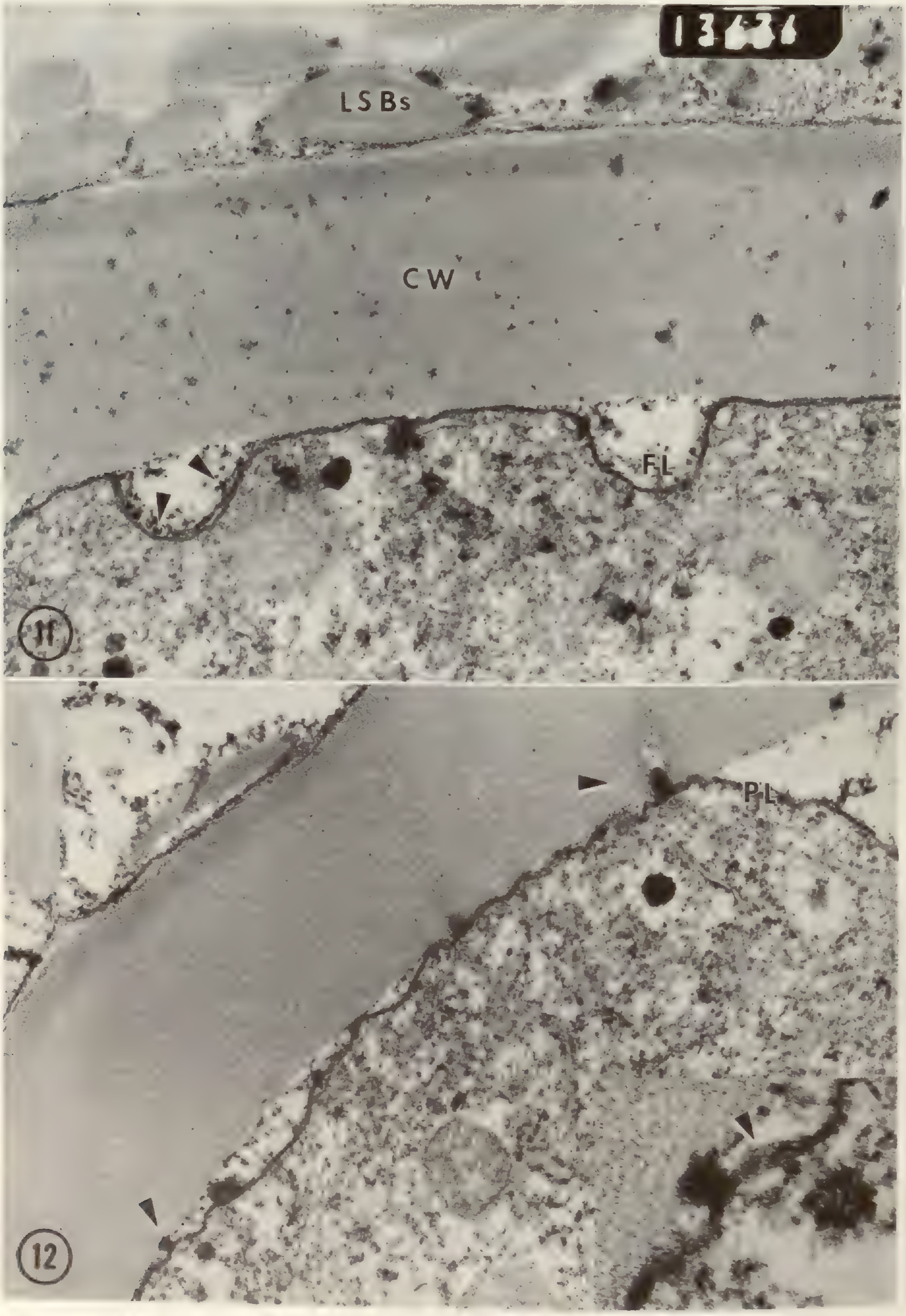
nels through the outer intine. In later stages of channel formation the openings extend through the outer intine to the base of the exine or to the surface where the exine has been sloughed (Fig. 30). The cytoplasm has abundant mitochondria and Golgi apparatus at this stage and the rough ER is tangentially aligned near the region of active intine development. The channeled layer of the intine (L1 layer) appears to thicken after the initiation of channel formation (see Figs. 30–31). At the completion of this thickening, the remaining vesicles become tangentially oriented and concentrated. The vesicles subsequently collapse and disintegrate to form a faint boundary between the foot layer at the base of the channels (L2) and the more extensive fibrillar layer below (Fig. 32: L3). The mature sporoderm on the distal hemisphere has, then, four recognizable layers (Fig. 33): the remnant exinous spinules; the thick channeled intine (L1); the L2 layer with more or less radially oriented fibrils at the base of the channels; and the L3 layer with tangential microfibrils that are appressed to the plasmalemma.

Development of the proximal intine (Figs. 34–36) is less rapid and elaborate than events on the distal side of the pollen grain. Loosely arranged microfibrils are the first signs of a proximal intine (Fig. 34), while at the same time the distal intine shows two layers (Fig. 28). By the time the proximal intine develops an outer compacted layer of microfibrils and an inner layer of loosely arranged microfibrils (Fig. 35), the distal intine has well-developed channels (Fig. 32). The mature sporoderm on the proximal hemisphere has a smooth, uninterrupted exine and a two- to four-layered intine due to different degrees of compactness of the microfibrils (Fig. 36).

Discussion

The biology of pollen becomes "curiouser and curiouser"[3] as new techniques and insights are brought to bear. No longer can one feel comfortable with Maheshwari's statement that the "development of the male gametophyte is remarkably uniform in angiosperms" (Maheshwari, 1950). Certain basic similarities are evident in the ontogeny of *Artemisia* (Rowley & Dahl, 1977) and *Heliconia*, for example, but pollen is proving as quixotic as most other biological features. "The new biology of pollen," as Vasil (1973) has called it, employs a host of sophisticated techniques to explore development, differentiation, and physiology of pollen grains, especially as they function in their natural environments. The biochemistry of pollen (Mascarenhas, 1975) and particularly the interaction between pollen grains and the stigmatic surface (Clarke & Knox, 1978) are providing insight into the more conspicuous pollen features that have deep-seated significance. The angiosperm pollen wall, for example, appears to be "adapted to carry physiologically active materials derived from the sporophytic parent (the exine domain), and the gametophyte itself (the intine domain)" (Heslop-Harrison, 1976). Since *Heliconia* has an elaborate intine with well-developed channels, there is a potentially large storage reservoir for compounds active in pollen germination and incompatibility. An understanding of the development of the spo-

[3] Dodgson, C. L. 1865. Alice's Adventures in Wonderland. By Lewis Carrol (pseud.). Macmillan and Co., London.



FIGURES 11–12. Primexine formation on the distal hemisphere, *Heliconia* "Ecuador," ×30,000.—11. Fibrous layer (FL) and plaques (arrows) initiated within plasmalemma invaginations adjacent to the peripheral callose walls (CW); LSBs of tapetal origin to the exterior.—12. Probacula development (arrows) sandwiched between plasmalemma (PL) and callose wall; faint hint of development of white lines (arrow) by "ballooning" of the plasmalemma (inset).

roderm of *Heliconia* is important to this problem, as well as to the more general question of how the ontogenetic pathway differs from the norm, where extensive exine elaboration is the case.

GRAIN POLARITY

Our initial question about the nature of heteropolarity in *Heliconia* pollen grains has been answered. The channeled intine region through which the pollen tube emerges (Kress et al., 1978: fig. 20) is located on the distal hemisphere. The evidence for establishing polarity actually comes from using the spinules as markers. In an attempt to identify nascent intine channels in mature tetrads, we soon discovered the well-known fact (see Heslop-Harrison, 1968a) that intine development is initiated in the free spore period following breakup of the tetrad (Fig. 5). Fortunately, the exinous spinules are concentrated on the same hemisphere as the channels (Kress et al., 1978: fig. 10) and their development occurs during the tetrad period. The spinules stud the primexine on the outer distal face of each microspore just prior to complete dissolution of the callose wall and subsequent intine formation (Figs. 13–14). These data confirm Erdtman's earlier speculation on the distal placement of the "ulceroid aperture" (Erdtman, 1966). The heteropolarity of *Heliconia* is unique among its close relatives, and there are few clues to its evolutionary history. In genera such as *Musa, Phenakospermum, Strelitizia,* and *Canna,* where the grains are isopolar, it is easy to envisage progressive localization of the radially oriented channels, the culmination of which is a species such as *H.* "Peru" in which the aperture is confined to the distal hemisphere (Fig. 2).

SPORODERM DEVELOPMENT

The pattern of sporoderm development is reasonably well known for a spectrum of angiosperms, based on papers by Echlin & Godwin (1969), Heslop-Harrison (1963, 1968a, 1968b, 1971a, 1971b), Horner & Lersten (1971), Horner & Pearson (1978), Rowley & Dahl (1977), Skvarla & Larson (1966), and others. Most attention has been directed to the ontogeny of the exine and for this reason Heslop-Harrison (1971a) was able to say that the "main morphogenetic activity is confined, then, to the tetrad period." While this statement is not applicable to *Heliconia* because of the intensive post-tetrad development of the intine, the general pattern of sporoderm development during the tetrad stage (Fig. 5) is similar to reports on other monocotyledons (*Lilium*: Heslop-Harrison, 1971b; *Tradescantia*: Mepham & Lane, 1969a; *Zea*: Skvarla & Larson, 1966) and dicotyledons as well (*Citrus*: Horner & Lersten, 1971; *Helianthus*: Horner & Pearson, 1978; *Parkinsonia*: Larson & Lewis, 1962; *Silene*: Heslop-Harrison, 1963).

The tetrads of *Heliconia* are large and particularly amenable for ontogenetic studies. The special callose wall of *Heliconia* is prominent at maturity (Fig. 9) and unlike *Pergularia* (Asclepiadaceae), the poor development of the exine cannot be attributed to the absence of callose (Vijayaraghavan & Shukla, 1977). The callose is finely granular and the sheath surrounding the tetrad shows an outer dark electron-dense band and an inner lighter band (Figs. 8, 11–12). The partitions between young microspores have a dark mid-line (Fig. 9) that corresponds to the

region of the "plaque cellulaire" (pc) in *Tradescantia* (Horvat, 1966). This stratified callose pattern can be accounted for by assuming that the initial formation of an enveloping callose sheath is followed by alternating periods of cell division and callose deposition: callose sheath; pc_1 in telophase I; callose around each diad; pc_{11} in telophase II; callose around each microspore. The number of visible callose wall stratifications depends on the age of the tetrad; the callose layers in older tetrads blend into one another. In this model, the outer tetrad wall is fundamentally 3-layered, the septa consisting of the pc_1 are 5-layered, and the pc_{11} septa are 3-layered. This sequence of development appears to be compatible with the drawing of a young tetrad of *Ipomoea* by Beer (1911) and the TEM micrographs of *Tradescantia* by Horvat (1966: fig. 4) and preliminary studies we have made on *Tapeinochilos* (Costaceae). Young tetrads of some species of *Heliconia* have cytomictic channels transversing the outer callose wall (Fig. 10). However, we have no evidence for cytoplasmic continuity between the tapetum and microspores; the deposition of callose prior to leptotene normally seals off all channels and isolates the microspores during subsequent pollen development (Echlin & Godwin, 1968b; Eschrich, 1963; Heslop-Harrison, 1966).

PRIMEXINE

The first evidence of sporoderm development follows meiosis and the envelopment of each microspore in callose (Fig. 5). The callose is thought to be impermeable to most macromolecules, thus assuring isolation of the developing male gametophyte (Vasil, 1973). The plasmalemma of each microspore is tightly appressed at first to the surrounding callose. Localized invaginations appear on the distal hemisphere of *Heliconia* and a fibrous layer and electron-dense plaques constituting young probacula develop in the plasmalemma pockets (Fig. 11). Heslop-Harrison (1968b), Larson & Lewis (1962), and Skvarla & Larson (1966) have commented on the uneven withdrawal of the plasmalemma from the callose, but there has been some question whether this is due to artifacts of fixation. We concur with the findings of Roland-Heydacker & Cerceau-Larrival (1975) in *Trachymene* (Umbelliferae) that the invaginations are part of the normal sequence of development and are the result, probably, of localized pressures exerted against the plasmalemma layer by a thickening fibrous layer (Dickinson, 1970). These pockets in *Heliconia* are confined to the distal hemisphere oriented towards the tapetum (see Heslop-Harrison, 1962), as are the probacula and mature spinules to which they give rise. The radially oriented probacula appear to enlarge by condensation of homogenous electron-dense material (glycocalyx of Rowley & Skvarla, 1975) around the plaques (Fig. 5), rather than by aggregation of sacs as in *Lilium* (Dickinson, 1970), or the formation of a "tridimensional network" as in *Canna* (Rowley, 1976; Rowley & Skvarla, 1975). The developing probacula

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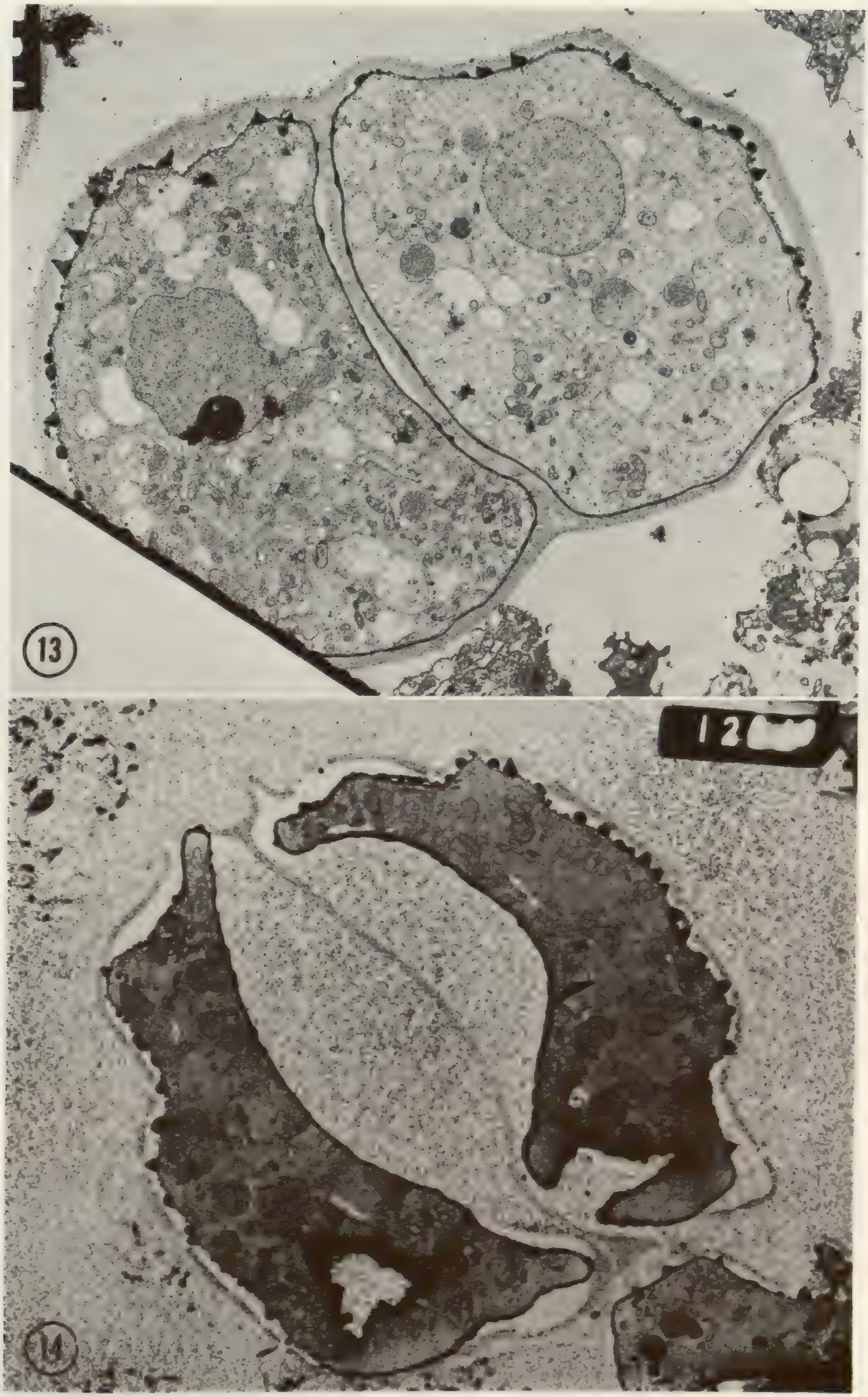
FIGURES 13–14. Maturation of primexine, *Heliconia nutans*, ×3,000.—13. Mid-probaculum stage with callose intact around and between microspores; primexine layer thin but continuous, nascent spinules localized on the outer, distal hemispheres.—14. Late-probaculum stage showing dissolution of surrounding callose; probacula (nascent spinules) reach maturity on distal face, while the smooth primexine on the proximal face is thickened slightly.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of *Heliconia* which appear similar to the "tufts" of *Artemesia* (Rowley & Dahl, 1977) definitely have a plasma membrane origin as determined in *Helianthus* by Horner & Pearson (1978) and *Lilium* by Dickinson (1970) and Dickinson & Heslop-Harrison (1968). The spinules of *Canna* also have a plasmalemma origin, but Rowley & Skvarla (1975) have refrained from employing the term "probaculum." Even so, it seems highly likely that we are talking about the same structure. The formation of probacula in *Heliconia, Helianthus* (Horner & Pearson, 1978), *Helleborus* (Echlin & Godwin, 1969), *Ipomoea* (Godwin et al., 1967), *Zea* (Skvarla & Larson, 1966) and others (see Heslop-Harrison, 1971a; Mascarenhas, 1975) marks the completion of the primexine phase of development. In *Heliconia* and *Canna* (Rowley & Skvarla, 1975), at least, the primexine template is an exact replica of the mature exine. Assuming that the intact callose wall is, in fact, impermeable to tapetal macromolecules (see Rodriguez-Garcia, 1978, for evidence to the contrary), sporophytic control of the exine pattern must reside in cytoplasmic information contributed by the microspore mother cells at meiosis prior to encapsulation of the tetrad in callose (Heslop-Harrison, 1971b).

WHITE LINES

Short segments of unit-membrane dimension appear in the early stage of probaculum development in *Heliconia* (Fig. 12). There has been active discussion about the formation, composition and function of the white line (Godwin et al., 1967), low dense line (Rowley & Dunbar, 1967), membranelike lamella (Rowley & Southworth, 1967), lamella (Dickinson & Heslop-Harrison, 1968; Heslop-Harrison, 1971a), primordial lamella (Nabli, 1975), or white line centered trilamellation (Rowley & Dahl, 1977). White lines are electron translucent ribbons of unit-membrane dimension (50–60 Å: Heslop-Harrison, 1971a; Rowley, 1962) that are sandwiched between two dark lines of approximately equal thickness. Rowley & Dahl (1977) discuss the evidence for a lipoprotein or phospholipid composition and the fact that the white line in *Artemisia* is the base plate for initiation and growth of the bacula. Probacula initiated during the tetrad period in *Heliconia* and most other genera have been found to stem from the plasmalemma (Flynn, 1971). The white lines are initiated at the base of the probacula and to the exterior of the plasmalemma. They are normally oriented tangentially, although occasionally a single white line passes radially into the center of a *Heliconia* probaculum (Fig. 21). The anomaly of *Artemisia* is probably due to the fact that the primexine template of this complex, multitiered Compositae pollen grain is relegated to formation of the tectum, while a secondary superstructure of pillars (i.e., bacules of Rowley & Dahl, 1977) is initiated to the interior. Rowley and Dahl cite Nabli's (1975) work in the Labiatae as evidence for the hypothesis that the "white line centered lamellation [is] a primordial exine lamella with a distal ectexine-forming

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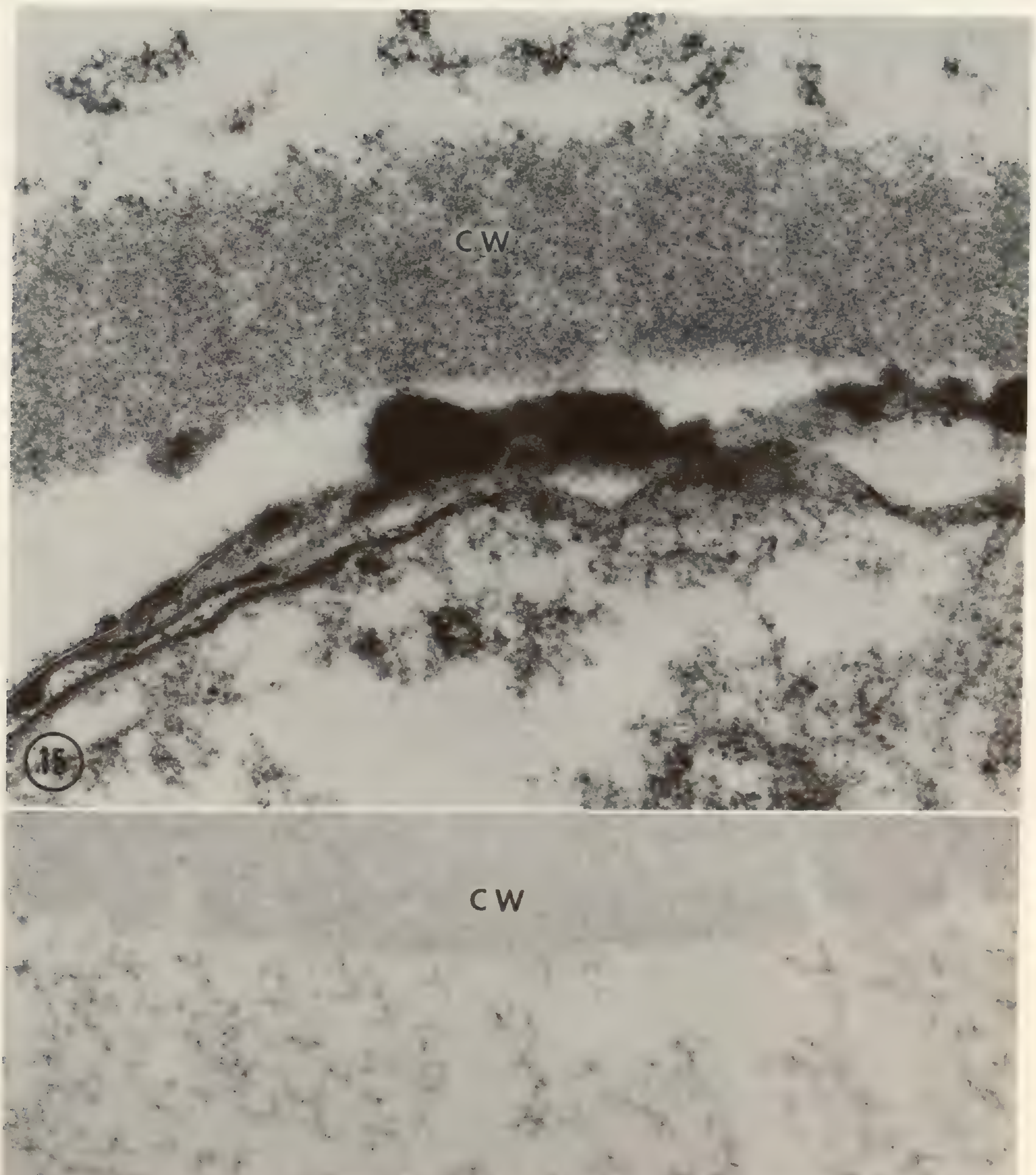
FIGURES 15–16. Protosporopollenin deposition on white lines, ×60,000.—15. Deposition concentrated at probacula sites during the tetrad period when the callose wall (CW) is intact, *Heliconia nutans*.—16. Outermost white lines become heavily coated with protosporopollenin from microspore protoplast, FAA preserved, *H.* "Peru."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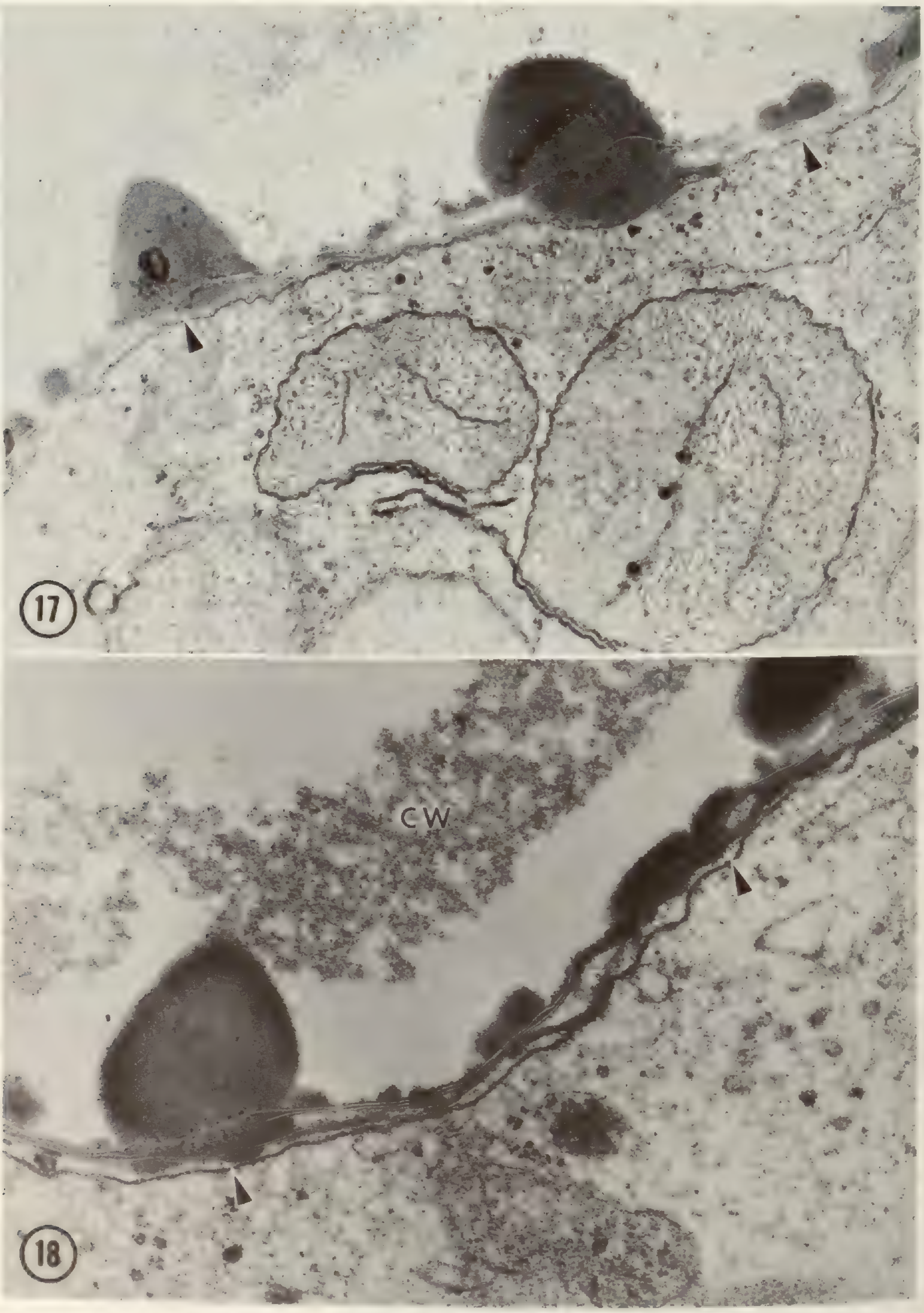


FIGURES 17–18. Late probaculum formation, *Heliconia nutans*—17. Proliferation of white lines to exterior of the plasmalemma (arrows), mainly situated at the base of nascent spinules, occasionally passing through the central region; large plastids mainly peripheral in the microspores, ×30,000.—18. Protosporopollenin from microspore layed down exterior to the plasmalemma (arrows) on a template of 4–5 white lines prior to disappearance of the callose wall (CW), ×40,000.

face (L1 of Nabli) and proximal endexine-forming face (L2)'' (Rowley & Dahl, 1977). It seems clear from Nabli's photographs (1975: plate I, fig. 2) that the probacula are well developed in the tetrad stage prior to the formation of a white line.

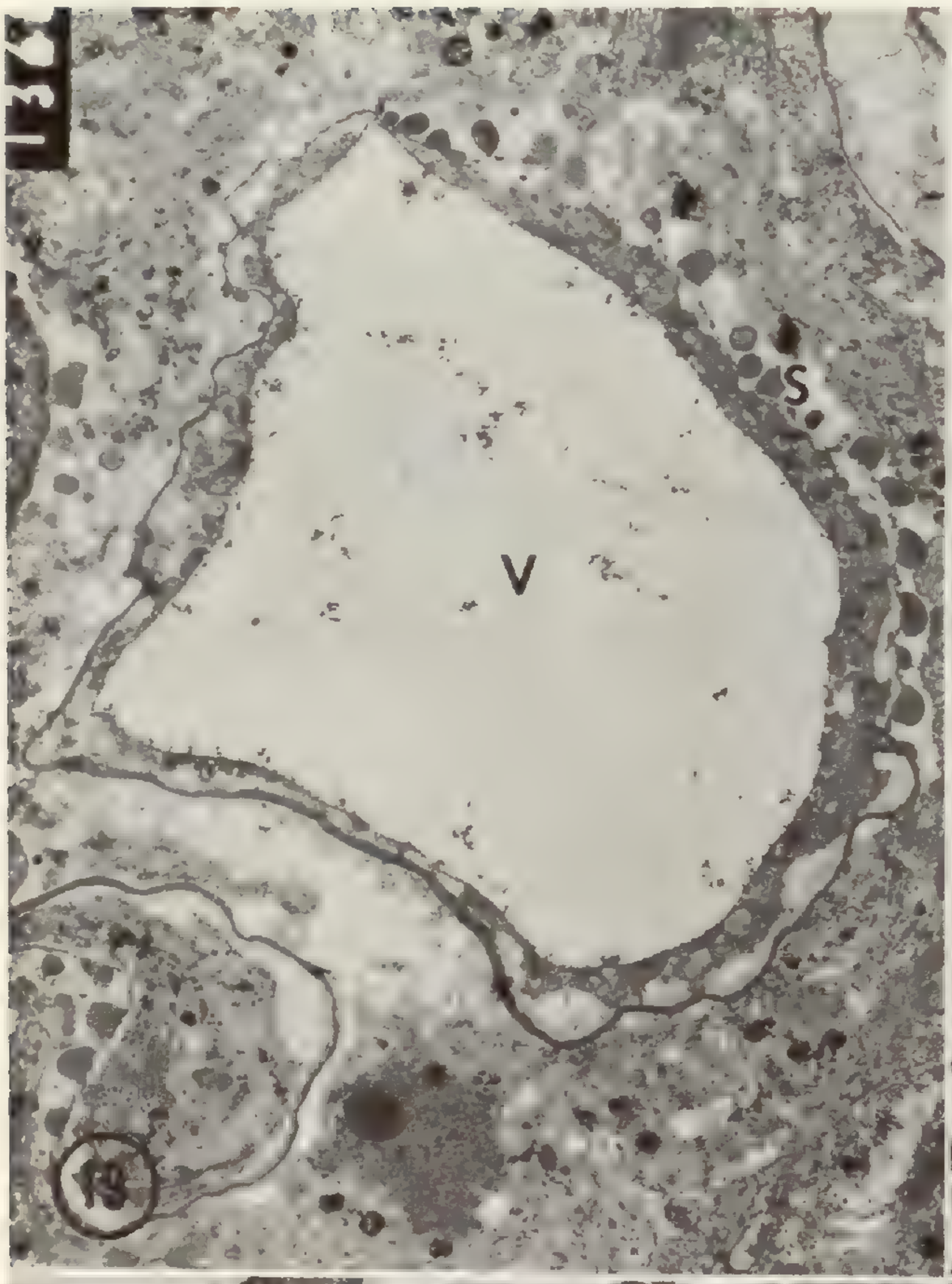
The earliest sign of white line formation in *Heliconia* appears as a localized proliferation or ''ballooning'' of the plasmalemma into multiple membranes (Fig. 12: inset). Our evidence for this is limited, but there is certainly no indication that the white line centered lamellation is synthesized ''far'' from the plasmalemma as inferred by Nabli (1975). Segments of the initial white line probably develop first beneath the probacula that are destined to become the largest and best anchored spinules. The young probacula apparently accumulate protosporopollenin to the exterior and interior of the initial white line, thus embedding the white line in the basal portion of the spinules (Figs. 17–18). As many as six white lines have been recorded on the distal face of *Heliconia* (Fig. 17) and four on the proximal hemisphere. The white lines form interrupted envelopes around the entire grain. While we have no chemical or physical confirmation of the nature of the white lines beyond the information derived from the TEM micrographs, one gets the distinct impression in *Heliconia* that the 30–40 Å thick white line is an entity unto itself, and its visibility is defined only by the presence of an electron opaque background. There is little question that the white lines serve as templates for deposition of protosporopollenin in *Heliconia,* not unlike the findings of Godwin et al. (1967) in *Ipomoea* and Rowley (1967) in *Anthurium* (also see Rowley & Dunbar, 1967).

Protosporopollenin accumulated adjacent to the exterior of the white line boundary gives rise to the amorphous-granular nexine-1 or footlayer (Heslop-Harrison, 1971b), while the white lines and deposits to the interior become part of the nexine-2 or endexine (Nabli, 1975), as for example in *Artemisia* (Rowley & Dahl, 1977) and *Helianthus* (Horner & Pearson, 1978). The common mode of origin for these two layers is apparent here as in *Lilium* (Dickinson & Heslop-Harrison, 1968), but the relatively poor subsequent elaboration of the exine in *Heliconia* precludes recognition of distinct exinous layers in the pollen at maturity (e.g., Fig. 36).

THE SECONDARY EXINE AND TAPETAL CONTACT

By the time the callose sheath begins to disintegrate in *Heliconia,* the nascent spinules are in place, white line development is complete and protosporopollenin deposition ceases. This is the period in most pollen grains when extracellular polymerization of the exine is mediated through sporopollenin precursors secreted in the thecal fluid by the tapetal cytoplasm (Heslop-Harrison, 1971a; Brooks & Shaw, 1978). *Heliconia* is different. The protosporopollenin may undergo further polymerization, but no significant amounts of sporopollenin are added to the primexine template. The secondary exine of *Heliconia* is, in effect, a mature primexine with white lines and a small amount of sporopollenin. There is, however, extensive contact with the tapetal discharge on the distal face and opportunity for interactions to occur.

The cell walls of the tapetum of *Heliconia* break down at the termination of meiosis and LSBs are released into the canals between adjacent protoplasts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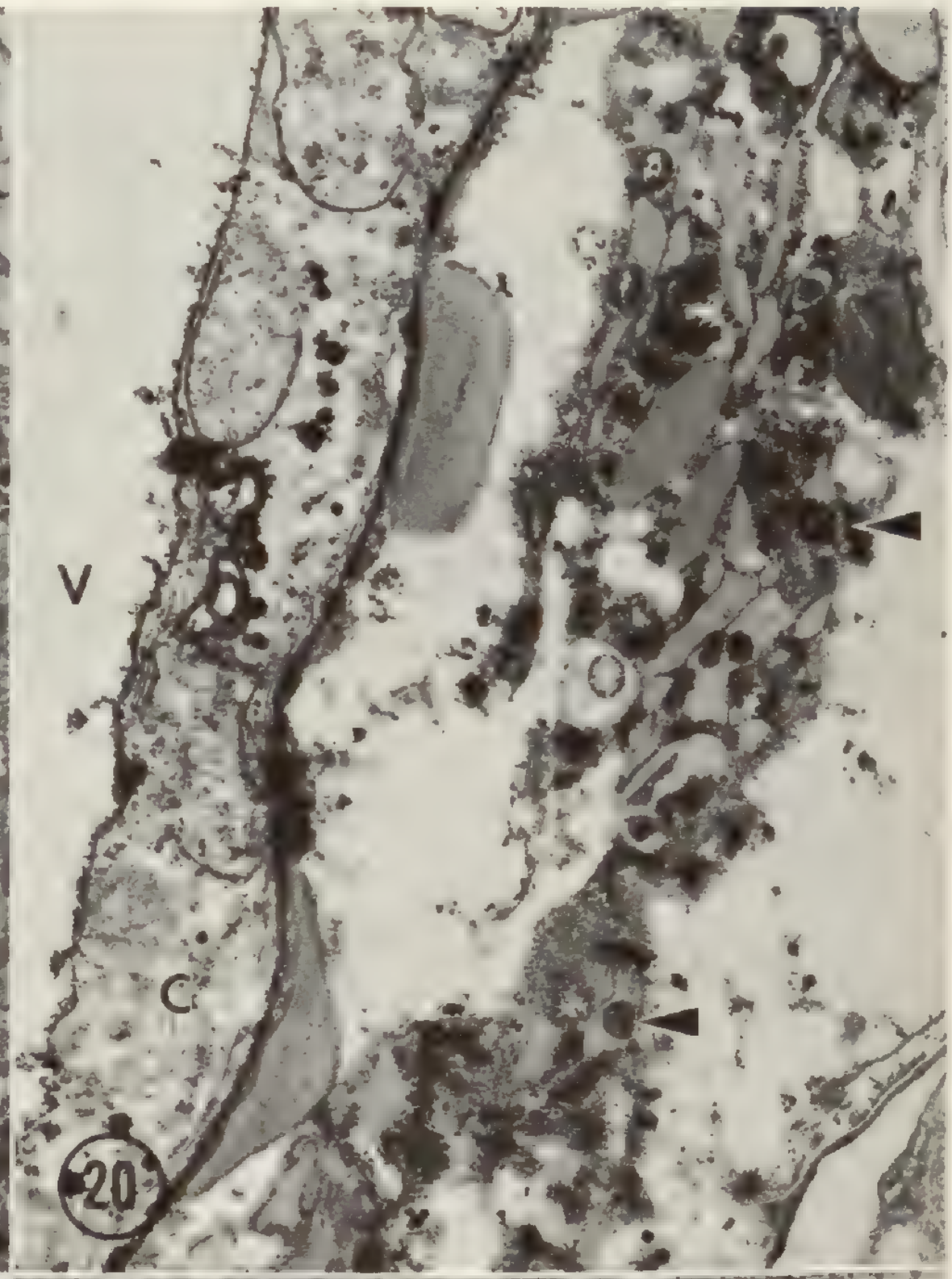
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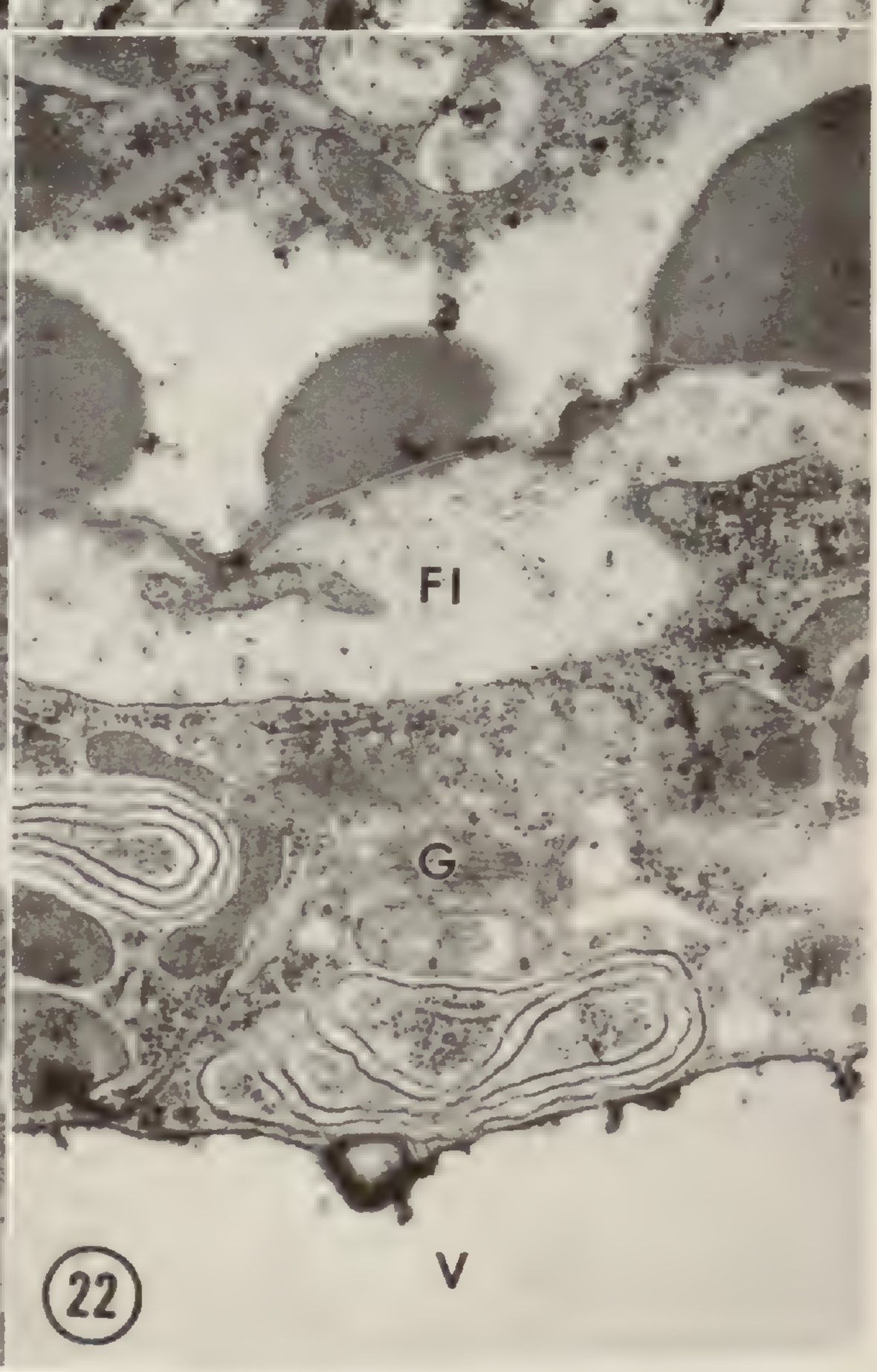
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(Fig. 8). The ultimate fate of the cells is to fuse to form an amoeboidlike tapetum (Fig. 19). This pattern of development is characteristic of the periplasmodium tapetum (Maheshwari, 1950) found in a minority of the angiosperms (Davis, 1966). Previous reports of an amoeboid tapetum in the Zingiberales include the Zingiberaceae (*Amomum* and *Nicolaia* only) and Cannaceae (*Canna*). The extensive contact of the periplasmodium with the developing microspores presumably enhances the nutritive function of the tapetum (Mascarenhas, 1975). The exact nature of the contribution of the tapetum is not known. In angiosperms with a glandular or secretory type of tapetum, orbicules or Ubisch bodies are common (Echlin & Godwin, 1968a). While these bodies have been suggested as the conveyors of sporopollenin from the tapetum to the incorporation sites on the exine (Echlin, 1971), their exact function is not clear and a direct connection with the developing exine has not been established (Mascarenhas, 1975). Species with a plasmodial tapetum such as *Tradescantia* (Mepham & Lane, 1969a) and *Heliconia* are not known to produce Ubisch bodies (Echlin & Godwin, 1968a; Heslop-Harrison & Dickinson, 1969). It is not entirely surprising, therefore, that Mepham & Lane (1968) suggest that the "exine is wholly a secretion of the pollen protoplast and that the tapetum makes no direct contribution to its development . . . ." Godwin (1968) has challenged their interpretation on the grounds of insufficient evidence, although he agrees that there is no substantiation of the claim that sporopollenin is pre-synthesized in the tapetum and transferred in particulate form to the exine. *Tradescantia*, like *Heliconia*, possesses tapetal-derived bodies that Mepham & Lane (1969b) refer to as lipid-globules. They are probably similar, if not identical, to the LSBs of *Heliconia*. These organelles do not, technically, qualify as Ubisch bodies because they lack the sporopollenin deposits characteristic of species with a secretory tapetum (Echlin & Godwin, 1969). However, like the lipid-globules, LSBs, pro-Ubisch bodies (Willemse, 1971) and gray bodies (Carraro & Lombardo, 1976; Lombardo & Carraro, 1976a, 1976b) are derived from the tapetal protoplast (Echlin, 1971). No internal structure is evident in these bodies until after they have been discharged from the tapetum into the anther loculus (see Echlin & Godwin, 1968a; Willemse, 1971). In the case of true Ubisch bodies, the acquisition of sporopollenin after tapetal discharge would provide the necessary electron-opaque background for visibility of the "streaks" or lamellae of white-line dimensions. Since the "streaks" become visible in the discharged lipoid globules of *Heliconia* and *Tradescantia* without sporopollenin deposits, some other process must be involved. It should be noted that many, but not all of the LSBs display prominent "streaks" (Figs. 8, 11).

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FIGURES 19–22. Free spore period, *Heliconia* "Ecuador."—19. Complete dissolution of callose wall and separation of microspores in the tetrad; rapid enlargement of microspore through formation of large central vacuole (V), forcing most organelles into a thick sheet of cytoplasm on distal face adjacent to spinules (S), ×2,500.—20. Disintegration of tapetum freeing protoplasmic contents with packets of ribosomes (arrows) and numerous LSBs, ×12,500.—21. Primexine template with several tangentially oriented white lines and occasional views of single radially oriented white lines penetrating the center of spinules; early formation of fibrillar intine (FI) between white lines (WL) and plasmalemma (PL), cytoplasm bounded on inner surface by tonoplast (T) of vacuole (V), ×25,000.—22. Fibrillar intine (FI) development associated with high ribosome content, Golgi apparatus (G) and complex folding of the ER within the protoplast, ×25,000.

23
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The role of LSBs and other tapetal products in the development of the secondary exine is by no means understood. Dickinson & Bell (1976) have determined that sporopollenin precursors are first released into the anther loculus of *Pinus banksiana*. Polymerization is preferential on lipoidal surfaces. Following meiosis, sporopollenin condensation occurs on lipid droplets to form orbicules on the lipid layer surrounding the loculus, and eventually on the primexine of the microspores when the callose walls dissolve. The LSBs of *Heliconia* are discharged from the tapetum into the loculus during the tetrad stage when the primexine is undergoing development (Fig. 11). The timing of release apparently differs in *Tradescantia,* for Mepham & Lane (1969b) speak of the production of lipid globules shortly after the microspores are released from the tetrads. Once the callose sheath of *Heliconia* disappears, the LSBs make close contact with the spinules and white lines (Figs. 23–24). There is some evidence here that short membrane segments with beads of ribosomal dimensions become attached to the primexine template. The significance of this to secondary exine growth in *Heliconia* is certainly inconsequential. However, the fact that there is direct physical transfer of tapetal-synthesized material substantiates the potential role of the tapetum in contributing to pollen development (Dickinson & Bell, 1976).

INTINE DEVELOPMENT

There is no evidence of intine in the young microspores until the exine is nearly mature. Following primexine formation in the tetrad and during secondary exine elaboration, the freed microspores expand nearly to the size of the former tetrad (Gaul et al., 1976; Heslop-Harrison, 1968b), and one large central vacuole normally flattens the cytoplasm into sheets and moves the nucleus to the periphery (Fig. 19). Sanger & Jackson (1971) found that several small vacuoles become positioned between the single furrowed aperture and the nucleus of the African blood lily. While they make the point that there is "no evidence . . . that a particular ultrastructural event can be causally related to the displacement of the nucleus prior to divisions," the formation of vacuoles would seem to serve this purpose. Whatever the precise role of vacuoles, the initiation of the intine is accompanied by microspore mitosis and tapetal disintegration (*Citrus*: Horner & Lersten, 1971; *Helianthus*: Horner, 1977; *Heliconia*: Fig. 22).

The intine is synthesized from within the microspore (Heslop-Harrison, 1968b) and the chemical composition differs in no essential way from the primary wall of somatic cells (Heslop-Harrison, 1971a; Sitte, 1953). While microtubules are present at this time, their small numbers and apparent lack of orientation in *Lilium* led Heslop-Harrison (1968b) to conclude that there is no evidence that they play a role in microfibril orientation. However, the prevalence of dictyosomes during intine formation (e.g., Roland, 1971: Ranunculaceae) is consistent with the view

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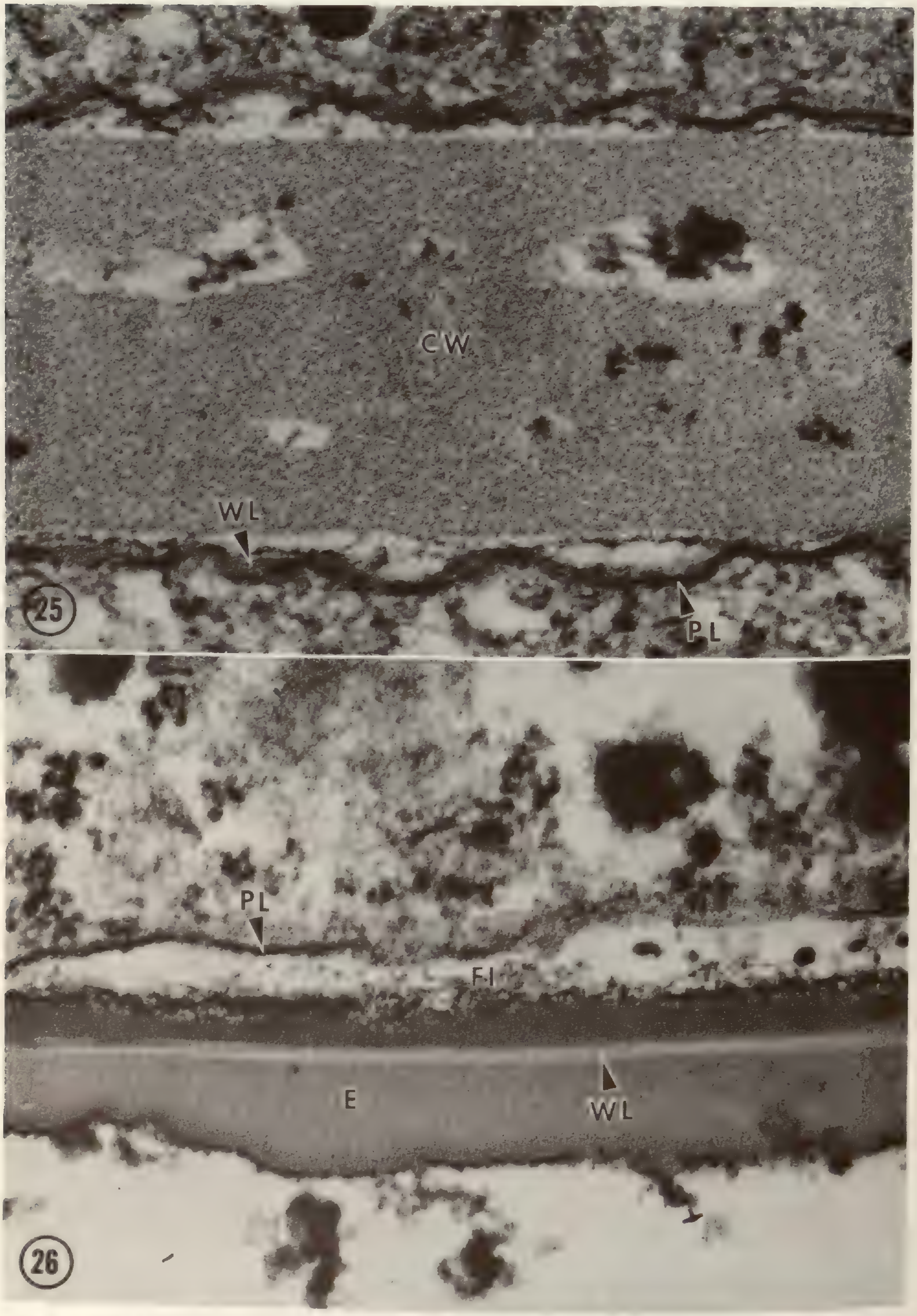
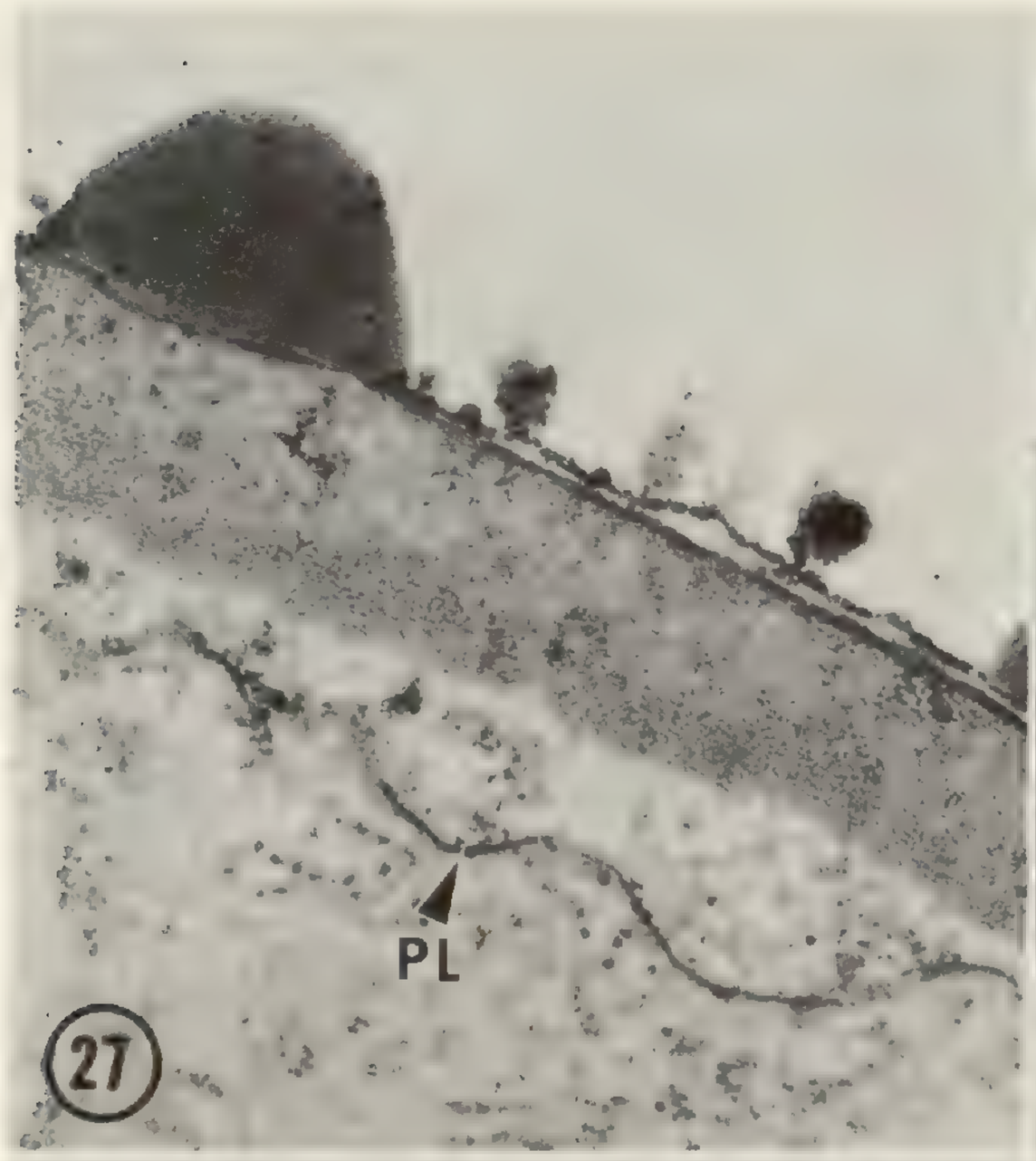
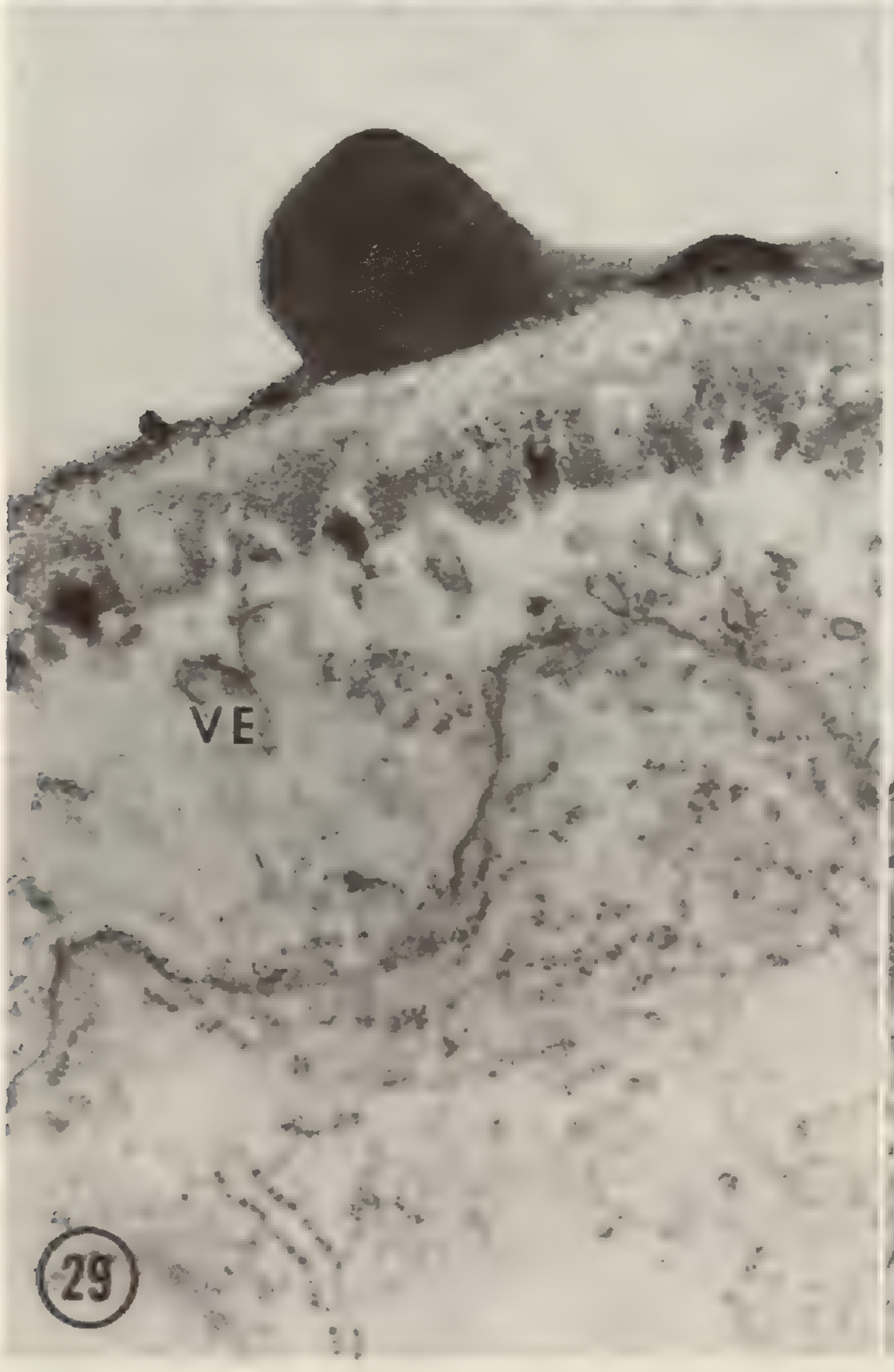
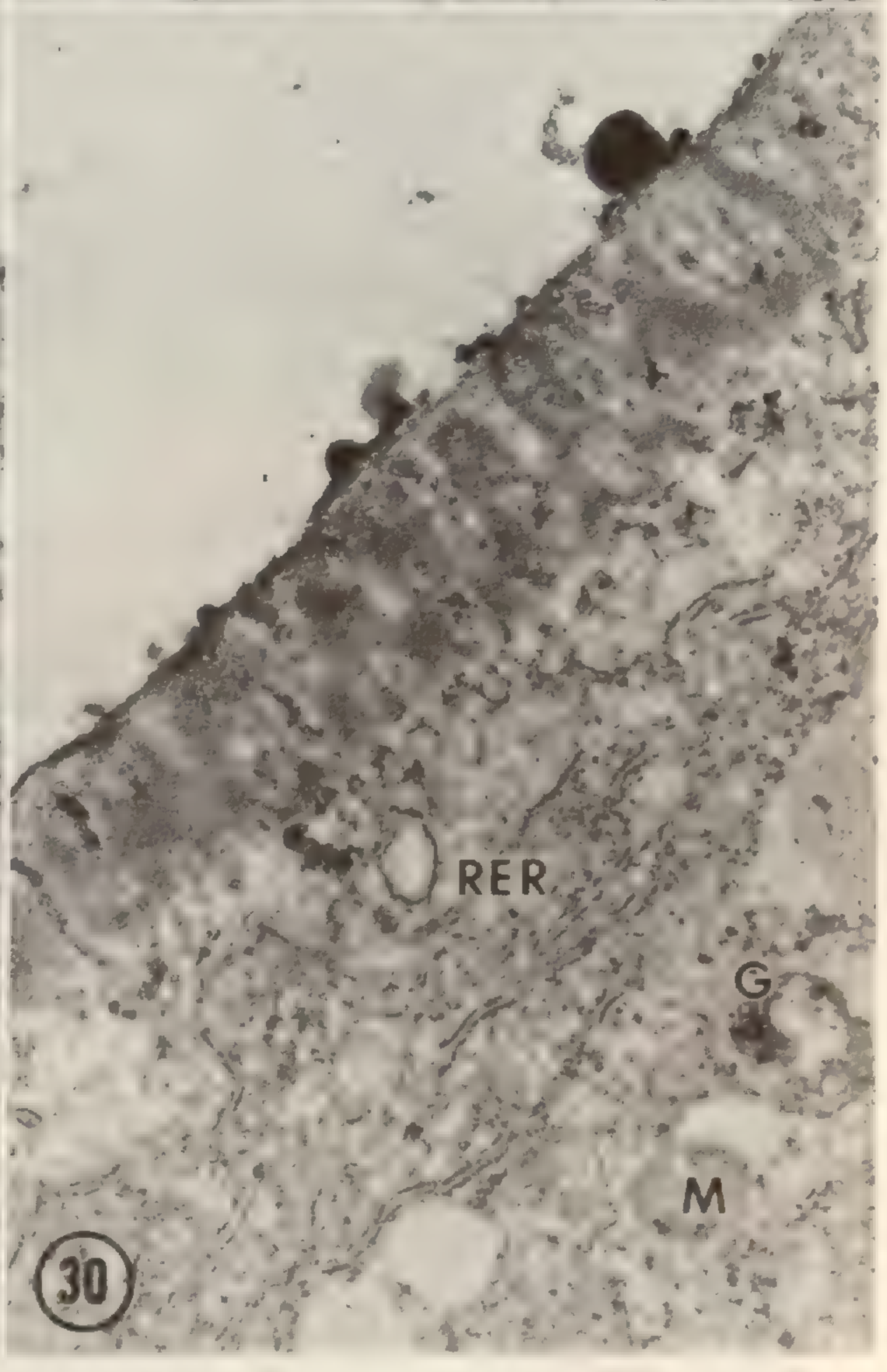
FIGURES 23–24. Maturation of the distal primexine to form secondary exine, *Heliconia* "Ecuador," ×80,000.—23. LSBs in vicinity of sporoderm associated with osmiophilic granules, presumably sporopollenin; ER fragments (arrows) with attached ribosomes appear to adhere to the outer surface of the primexine.—24. White lines of unit membrane dimensions may serve as template for ribosome attachment and sporopollenin polymerization.



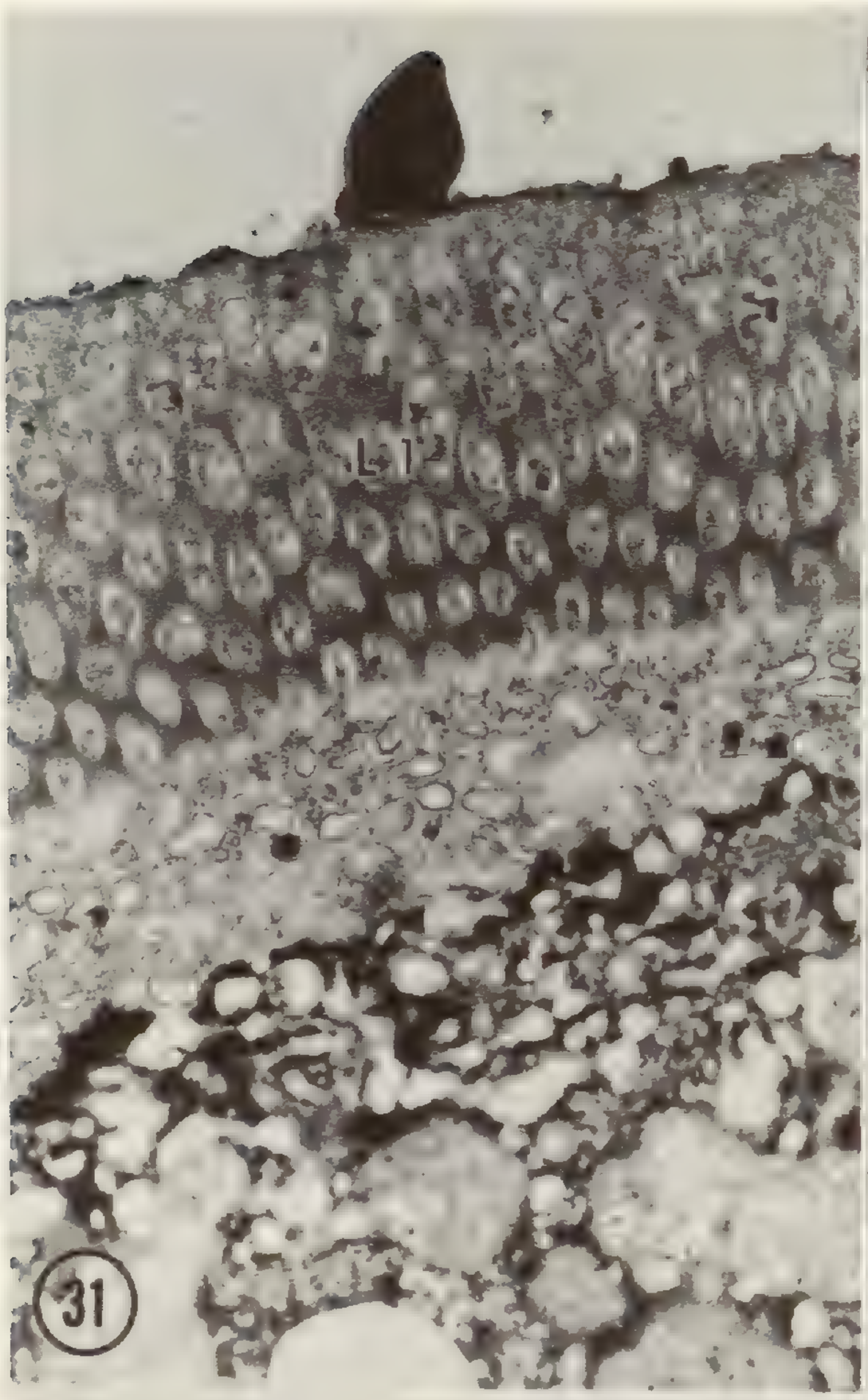
FIGURES 25–26. Ontogeny of the proximal exine, *Heliconia* "Ecuador," ×120,000.—25. Early probaculum stage, sister microspores separated by pitted callose wall (CW); evidence of white line formation (WL) to exterior of plasmalemma (PL).—26. Free spore stage showing mature exine (E), well-developed white lines (WL), and early development of fibrillar intine (FI) to exterior of plasmalemma (PL).







FIGURES 27–30. Early development of the distal intine, *Heliconia nutans*.—27. Fibrillar intine loosely arranged in a zone adjacent to the plasmalemma (PL) and compacted into a dense band near the periphery of the microspore; separation and sloughing of white lines appear imminent in areas between spinules, ×25,000.—28. Microspore cytoplasm appears particularly active in areas of intine buildup, plastids (P) and microtubules (MT) are in evidence and the plasmalemma is indistinct in places, ×25,000.—29. Radially oriented vesicles (VE) congregate in the loosely arranged fibrillar zone adjacent to the compacted intine and in association with the nascent channels, ×25,000.—30. Late channel formation through compacted intine, showing continuity between loosely arranged fibrillar zone and peripheral exinous surface; cytoplasm with concentration of tangentially oriented rough ER (RER), Golgi apparatus (G) and mitochondria (M), ×12,000.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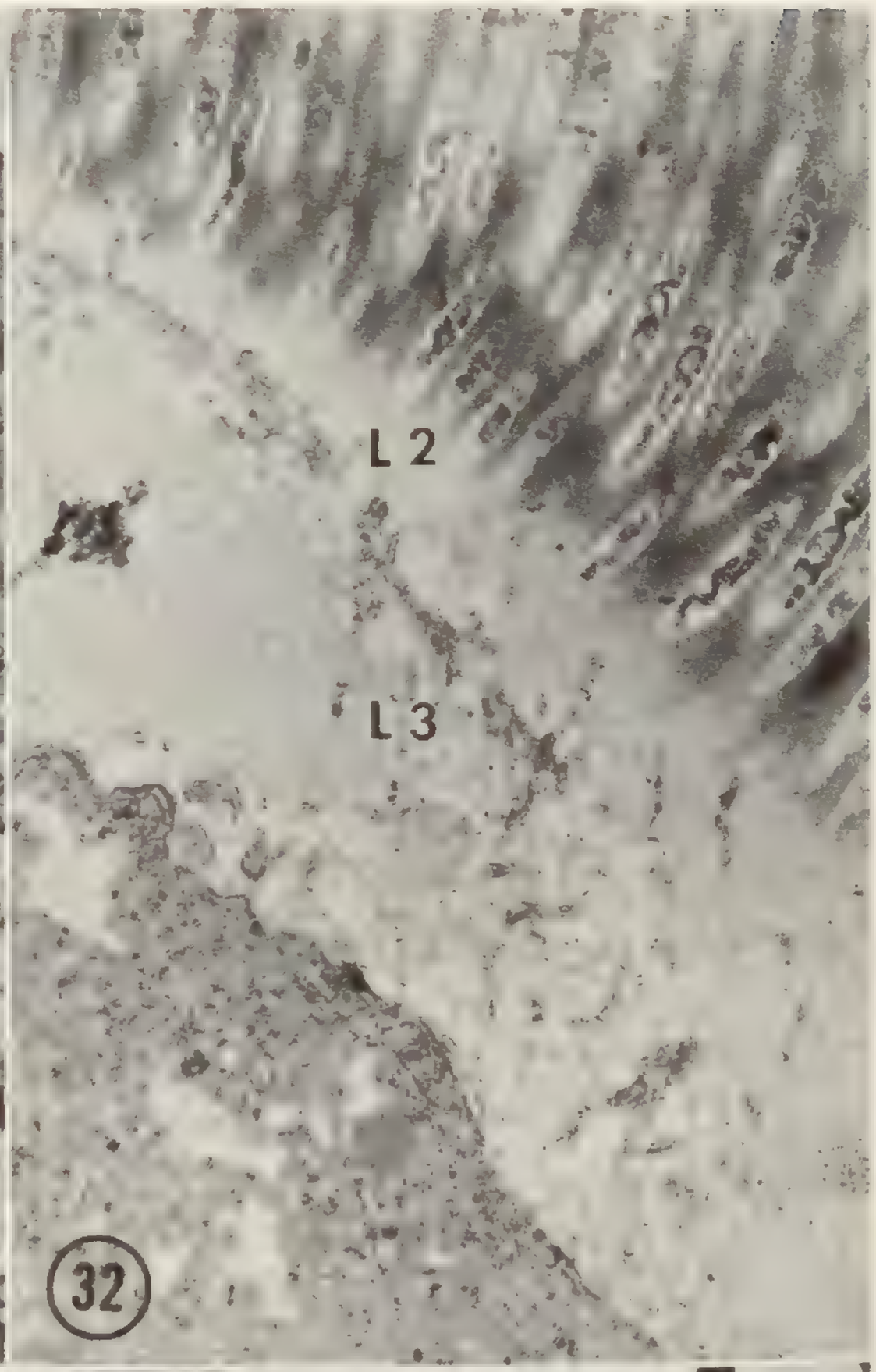
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that cytoplasmic vesicles penetrate the plasmalemma and discharge contents into the wall (Mühlethaler, 1967). Particles on the outside of the plasmalemma apparently complex with cellulose units to form microfibrils (Heslop-Harrison, 1971a). Intine growth proceeds in waves (Stanley & Linskens, 1974) and concentric lamellations are often present (*Heliconia*: Fig. 36; *Silene*: Heslop-Harrison, 1968a; as well as Musci: McClymont & Larson, 1964). In species such as *Silene* where there are defined apertures, the intine is initiated beneath the apertures and then development continues outward in a radial pattern (Heslop-Harrison, 1968a). Somewhat of the same situation prevails in *Heliconia*. The distal hemisphere which serves as the aperture region shows a more rapid and elaborate intine development than the proximal face.

Following the appearance of a loose weft of microfibrils in *Heliconia* (Fig. 21), the intine becomes compacted between the plasmalemma and the base of the exine (Fig. 27), similar to the situation Heslop-Harrison (1971b) described for the aperture region of "normal" pollen grains. Formation of the intine channels in *Heliconia* does not occur until after the microfibrils have been compacted (Fig. 27). Components are secreted through the plasmalemma to form radially oriented vesicles that become associated with the interior face of the compacted intine. These vesicles appear to be active in dissolving channels through the outer intine (Fig. 29). The development of channels (tubules) in *Crocus* has been equated with that of *Canna* by Heslop-Harrison (1977), and she surmises that they arise "by the development of microvilluslike extensions of the spore surface which later become encased by the polysaccharide material of the wall." To our knowledge, the development of the outer intine of *Canna* has not been investigated, although Skvarla & Rowley (1970) did comment that the intine channels of mature pollen grains are "membrane bound." Additional intine thickening does take place in *Heliconia* after the channels penetrate the outer layer, and it may well be that the vesicles become encased by the later-formed intine. The mature intine of *Heliconia* has prominent channels that may or may not be covered by a thin exinous coat. To the interior, the base of the channels is sealed by a thin layer of radially oriented microfibrils (L2) and a much thicker strata of tangentially oriented fibrils (L3). Rowley & Skvarla (1974) found that the outer intine of *Canna* (i.e., channeled region) is initiated soon after meiosis, while the inner intine is delayed until after microspore mitosis. They attribute the development of a lobed inner intine to the formation of "plasmalemmasome regions." The lobes are eventually compressed and the inner intine becomes flattened at maturity, "presumably because of cytoplasmic turgor and the general increase in volume of the protoplast" (Rowley & Skvarla, 1974). Lobes of plasmalemma undulations of this

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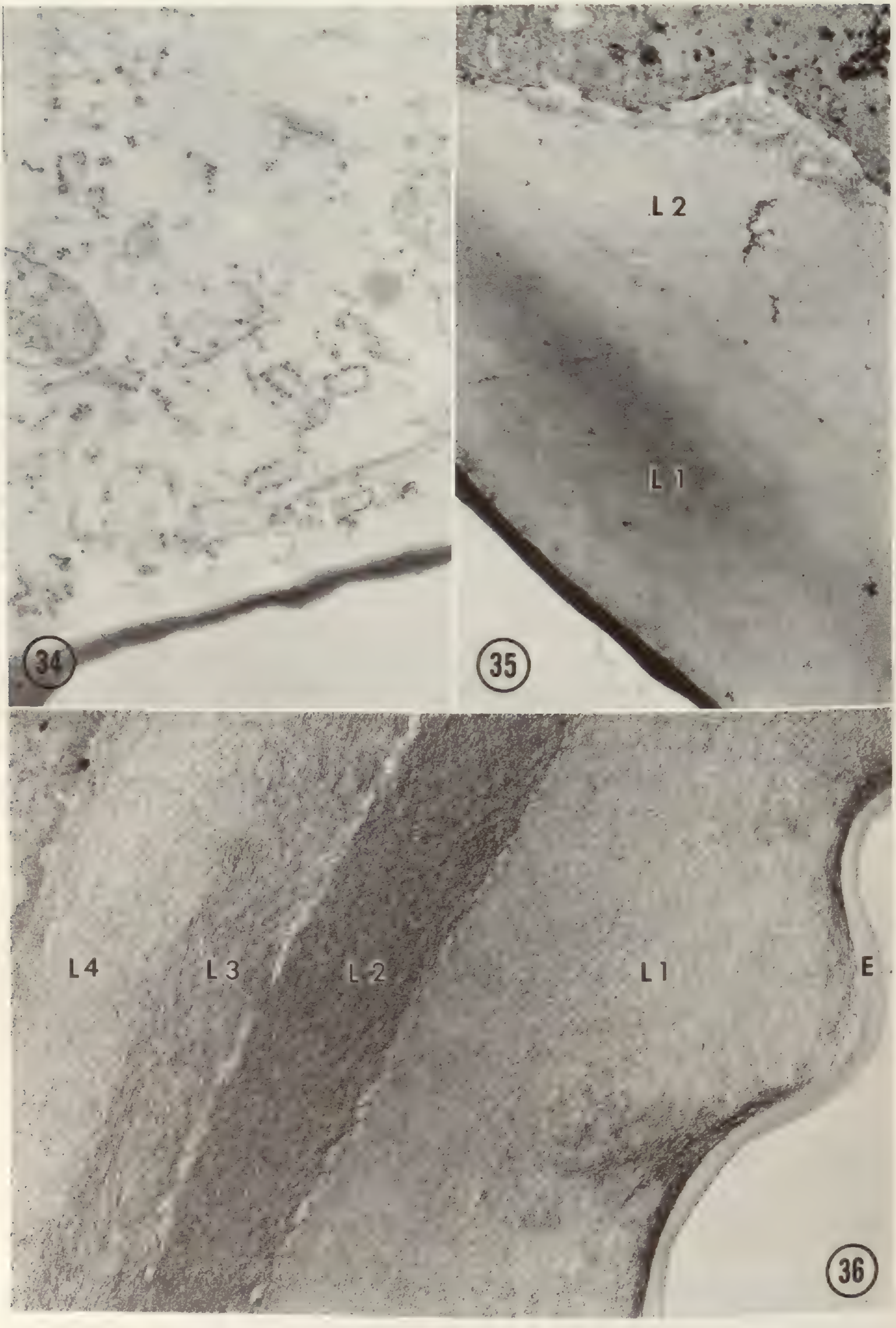
FIGURES 31–33. Maturation of the distal intine, *Heliconia nutans*.—31. Continued thickening of the channeled layer (L1), tangential alignment of the vesicles into a concentrated band, and disorganization of the adjacent cytoplasm, ×12,000.—32. Thickening of the layer (L2) at the base of the channels, collapse and distintegration of vesicles in the innermost layer of the intine (L3) and deposition of more or less tangentially oriented microfibrils, ×12,500.—33. Mature sporoderm, distal hemisphere: tenuously seated spinule(s) on fragmented exinous base (E); well-developed channels in L1 layer; radially oriented microfibrils in L2 base layer; and tangentially oriented microfibrils in L3 layer, ×30,000.



FIGURES 34–36. Ontogeny of the proximal intine, *Heliconia nutans*.—34. Early- to mid-stage of fibrillar intine development (comparable to distal intine development of Fig. 28) with loosely arranged microfibrils near exine; extensive development of rough vesicles and elongated microtubules. ×25,000.—35. Mid-stage (same microspore shown in Fig. 32 for demonstration of distal intine de-

sort are also evident in *Heliconia* during formation of the inner intine (Fig. 28). The plasmalemmasomes of Rowley and Skvarla may be similar to the degenerating vesicles we find associated with formation of the L2 and L3 strata of *Heliconia* pollen. The same course of development for the intine of *Canna* and the distal hemisphere of *Heliconia* is inferred from the similarity in the mature sporoderm. The only basic difference is that the spinules of *Canna* are loosely textured in a "tridimensional network" (Rowley & Skvarla, 1975), whereas those of *Heliconia* are finely granular and solid without apparent areoles.

The elaborate nature of the intine of such plants as *Crocus*, *Canna*, *Heliconia*, and the Caryocaraceae (Barth, 1966) makes one wonder about the possible adaptive significance. The works of Heslop-Harrison (1975) and Knox (Clarke & Knox, 1978), in particular, have established that the normal pollen wall has two functional domains, both of which have the potential to store proteins involved in germination and incompatibility reactions (see Knox, 1973, 1976). The sporophytic domain consists of interbacular spaces in the exine which serve as reservoirs for tapetal proteins, whereas the intine incorporates microspore-synthesized proteins in the gameophytic domain. Since plants with reduced exines lack the capacity for storage of tapetal proteins, it is not surprising that sporophytic incompatibility has not been discovered in the Zingiberales, or for that matter in any monocotyledons (Heslop-Harrison, 1976). Whether the elaborate intine in these plants functions in some special way in germination and gametophytic incompatibility is unknown. There is apparently no direct evidence that intine-borne proteins are involved in gametophytic incompatibility, although the stigmatic inhibition of the gametophytically controlled system in the Gramineae is suggestive of such a mechanism (Heslop-Harrison, 1978). More refined pollinator-pollen-stigma interaction studies are needed to determine the roles of exineless pollen in the Zingiberales.

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velopment), compact L1 layer, loosely arranged microfibrils in L2 layer, ×12,500.—36. Mature sporoderm (same stage and grain as in Fig. 33): exine (E) thin, but continuous; intine thick and stratified into 4 layers (L1–L4), ×30,000.

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COMPARATIVE POLLEN MORPHOLOGY OF THE AMERICAN MYRISTICACEOUS GENERA *COMPSONEURA* AND *VIROLA*[1]

JAMES W. WALKER AND AUDREY G. WALKER[2]

ABSTRACT

Pollen of the American myristicaceous genera *Compsoneura* and *Virola* was studied with light, scanning electron, and transmission electron microscopy. Formal generic pollen descriptions are provided for each of these genera. Study of the pollen of these two genera reveals that they possess a number of similar palynological features, including sulcate apertures, reticuloid to reticulate exine sculpturing that sometimes consists of banded or beaded muri, a columellate interstitium with columellae frequently hanging from the tectum or only weakly attached to the nexine, and tectate-perforate to semitectate pollen grains. Pollen of *Compsoneura*, however, can be distinguished from that of *Virola* by (1) its nexine which is generally twice as thick as that in *Virola*, (2) its consistently more or less solid, nonlamellate nexine, and (3) its consistently inconspicuous intra-exinous, sexinous cavities. Within *Compsoneura*, pollen of section *Coniostele* is decidedly more advanced than that of section *Compsoneura*. *Virola* exhibits a wide range of exine sculpturing patterns, allowing recognition of three basic pollen types. Species of Pollen Type I have basically tectate-perforate grains although sometimes their pollen may be more or less reticuloid, and the exine surface or muri are usually psilate. Pollen Type II is characterized by tectate-perforate to semitectate grains which have banded to beaded muri, while Type III pollen grains are semitectate-reticulate with psilate muri.

This is the fourth paper in a series dealing with the comparative pollen morphology of the family Myristicaceae. In previous papers we have already dealt with the pollen of the Madagascan (Walker & Walker, *Grana*, in press) and mainland African (Walker & Walker, *Amer. J. Bot.*, 1, in press) genera of Myristicaceae, and with the American myristicaceous genera *Dialyanthera*, *Iryanthera*, and *Osteophloeum* (Walker & Walker, *Amer. J. Bot.*, 2, in press). We are concerned in this paper with the pollen of the two remaining genera of American Myristicaceae—*Compsoneura* and *Virola*. We intend to examine the pollen of the Asian genera of Myristicaceae in subsequent papers.

In the most recent revision of the American Myristicaceae, Smith (1938) recognized 8 species of *Compsoneura* and 38 species of *Virola*. Since then 2 additional species of *Compsoneura* and 9 more of *Virola* have been described, so that at present there are 10 species of *Compsoneura* and approximately 50 species of *Virola*. *Compsoneura* and *Virola* range from southern Mexico to northern South America, where most of their species occur.

After the material and methods section, formal generic pollen descriptions are provided for both of the genera studied. This is followed by a discussion of the palynological features of these two genera, such as aperture type, exine sculptur-

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[1] We thank the directors of the following herbaria for allowing us to collect palynological material from their collections: Arnold Arboretum, Harvard University; Gray Herbarium, Harvard University; Royal Botanic Gardens, Kew; Botaniska Institutionen, Naturhistoriska Riksmuseet, Stockholm; and Rijksherbarium, Leiden. We are especially grateful to Keith Ferguson (Kew), B. Sparre, S. Nilsson, and J. Praglowski (Stockholm), and J. Muller (Leiden) for their help during our visits to their respective institutions. This work was supported by U.S. National Science Foundation grants GB-35475, BMS 75-10438 (subsequently DEB 75-10438), BMS 75-02883, and DEB 79-04213 to James W. Walker.

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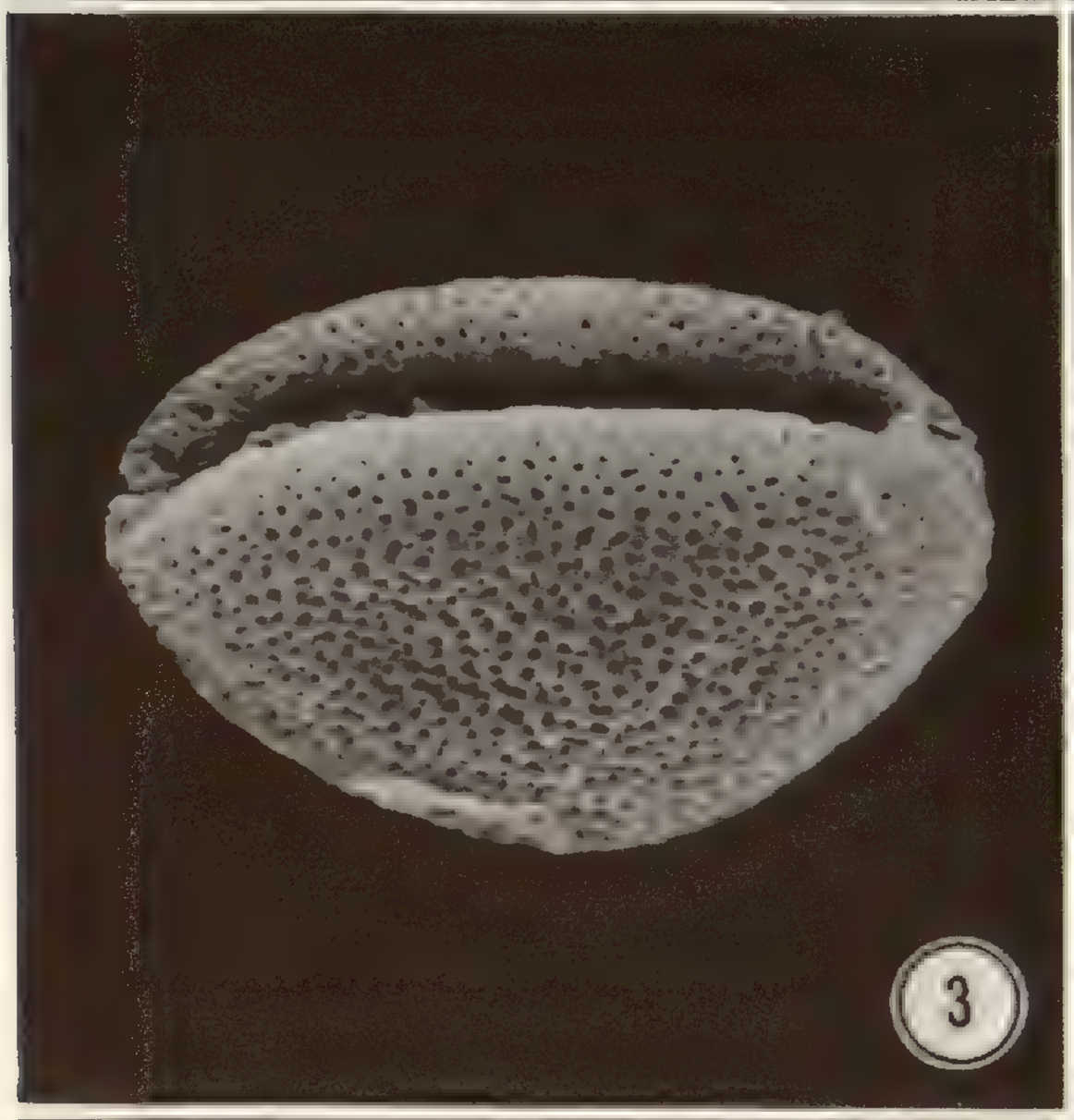
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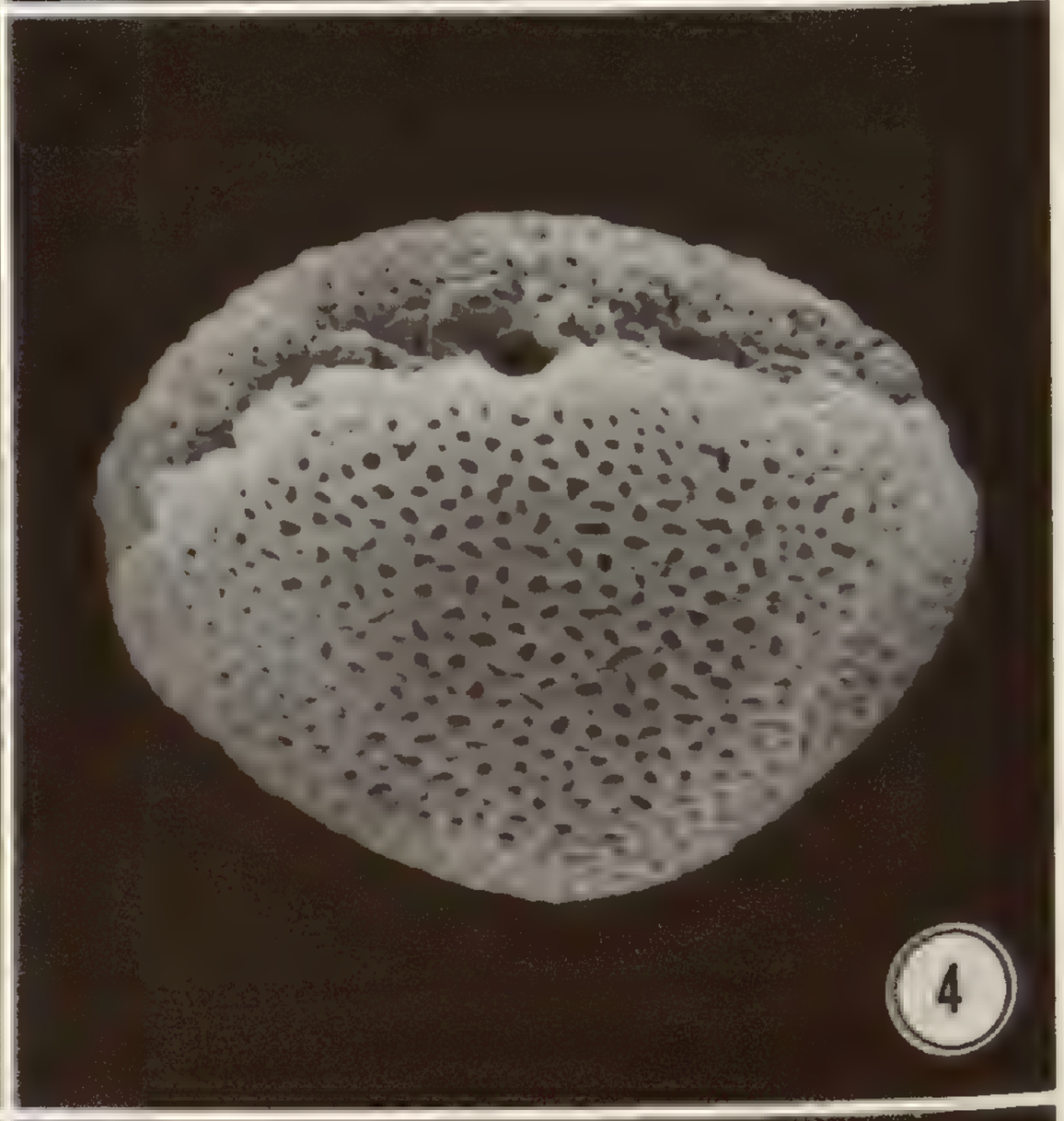
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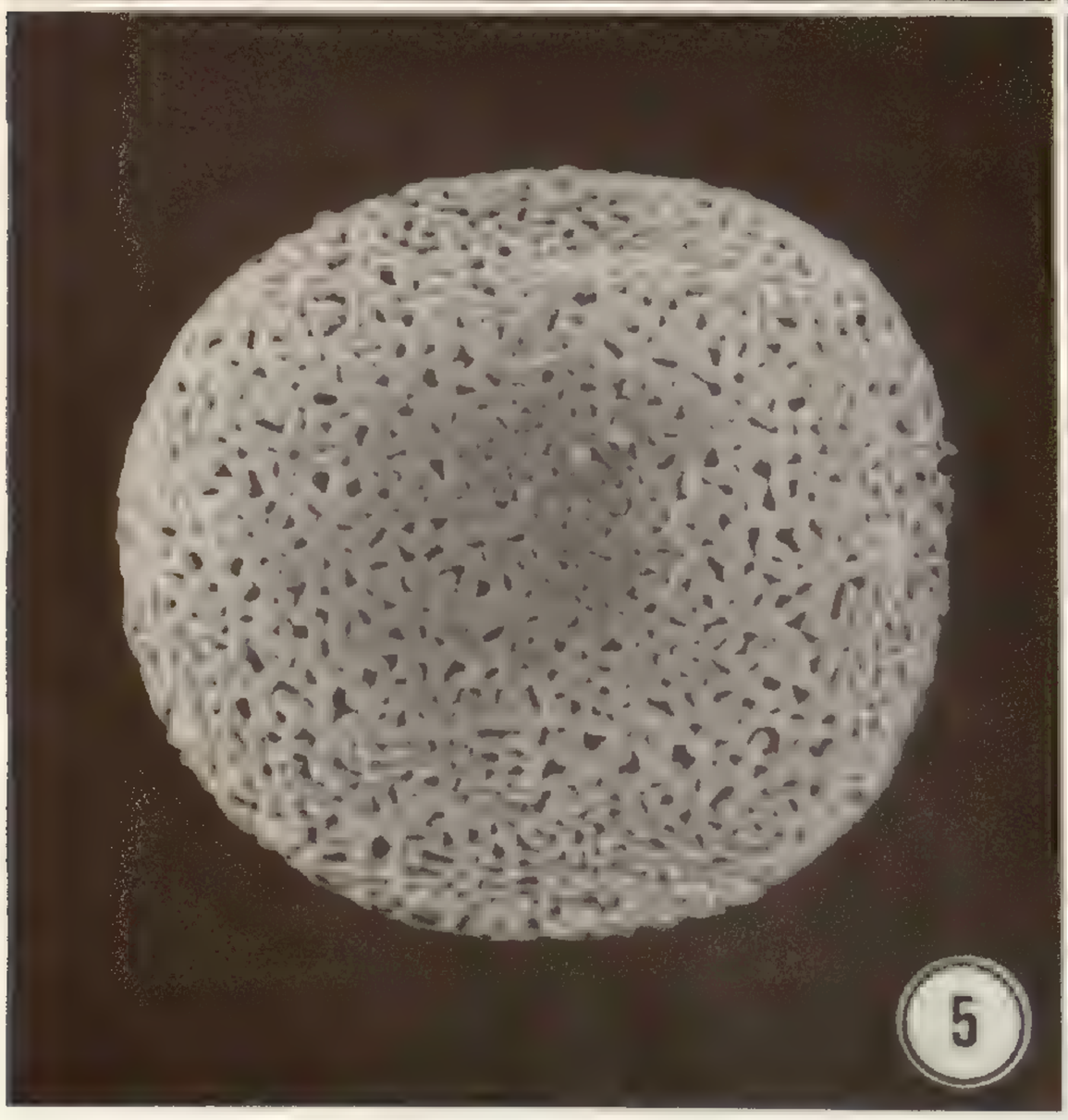
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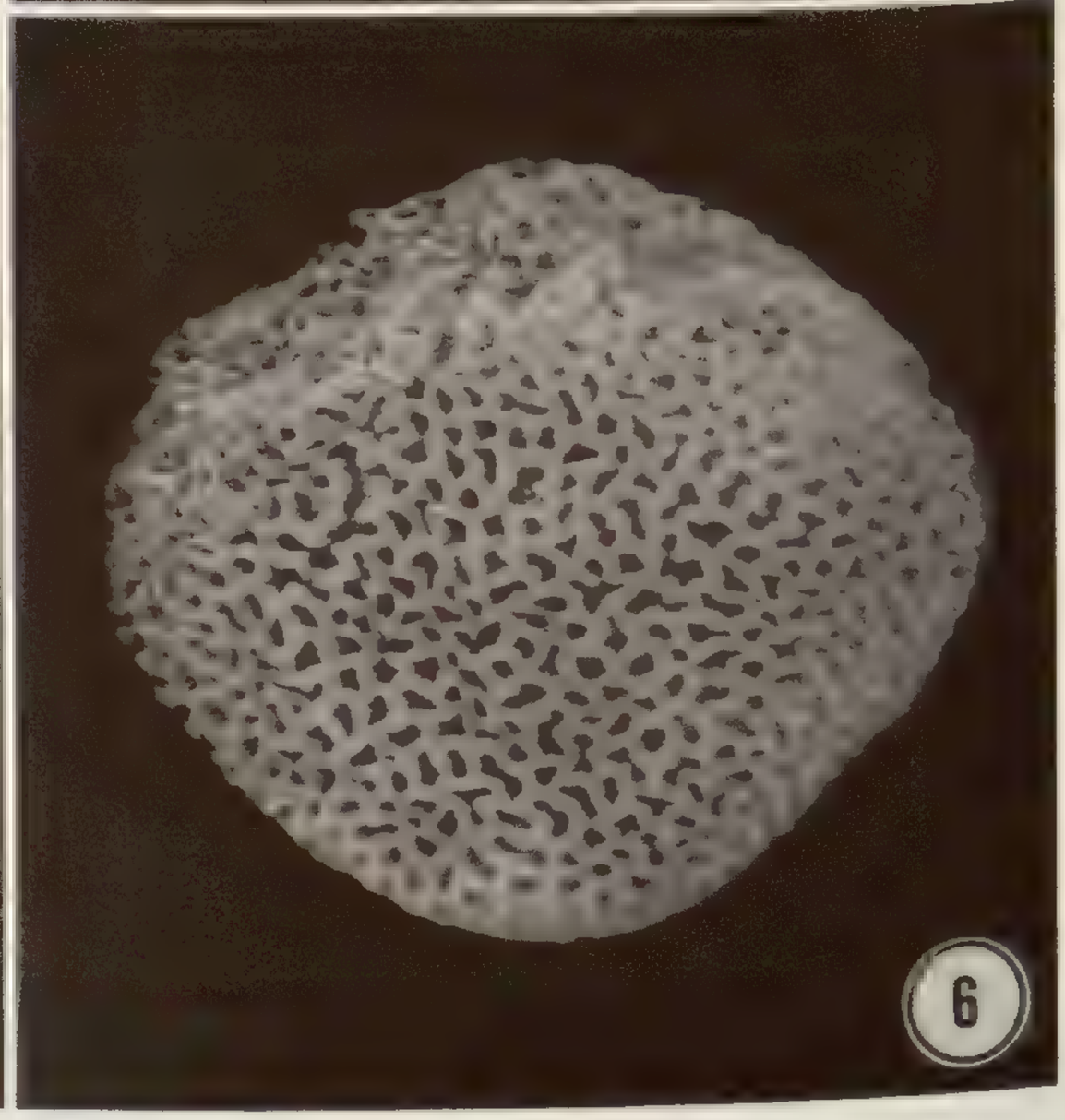
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ing, exine structure, and so forth. The pollen of *Compsoneura* is then compared as a whole with the pollen of *Virola* in the conclusions section of the paper.

Material and Methods

Pollen for study was taken from herbarium sheets at the Arnold Arboretum, Harvard University (A); the Gray Herbarium, Harvard University (GH); the Royal Botanic Gardens, Kew (K); the Botaniska Institutionen, Naturhistoriska Riksmuseet, Stockholm (S); and the Rijksherbarium, Leiden (L). Voucher specimens and the senior author's palynological accession number (preceded by a "p") are listed for each collection studied after the generic pollen descriptions, and indication is given if the pollen was studied by scanning electron microscopy of the surface (SEM) or of sectioned material (SEM-X) or by transmission electron microscopy (TEM). An attempt was made to study pollen from as many collections annotated by A. C. Smith or cited by him (Smith, 1938, 1950) as possible. In all we examined pollen of 7 of the 10 species of *Compsoneura* and 32 of the nearly 50 species of *Virola*. Terminology follows Walker & Doyle (1975), Walker (1974, 1976), and Walker & Walker (in press, 1, 2, 3).

Pollen was prepared for light microscopy, scanning electron microscopy, and transmission electron microscopy essentially by the same methods previously outlined (Walker & Walker, in press, 1, 2).

Generic Pollen Descriptions

Compsoneura Warburg (Figs. 1–24)

Pollen.—Apertures sulcate, sharply delimited externally. Shape usually boat-shaped, occasionally almost globose-spherical, frequently more or less triangular in outline and often more or less straight on the apertural face and markedly convex on the opposite face. Polarity heteropolar. Symmetry bilateral. Size medium-sized to small (mean 24 μm, range 21–27 μm). Pollen-Unit monads. Exine Sculpturing mostly reticuloid, less commonly definitely reticulate and then sometimes with finely banded muri. Exine Structure columellate (columellae weakly attached to the nexine), tectate-perforate or less commonly semitectate; nonapertural exine about 1.50 μm thick, with an average (about 32% of total exine thickness), essentially solid nexine, an average to moderately thick (about 39% of total exine thickness) interstitium, and an average (about 29% of total exine thickness) tectum, sexine infrequently with small, spherical, intra-exinous cavities; apertural exine with an extremely to very thin nexine and a greatly reduced and much disorganized sexine. Exine Stratification wholly ektexinous; endexine none.

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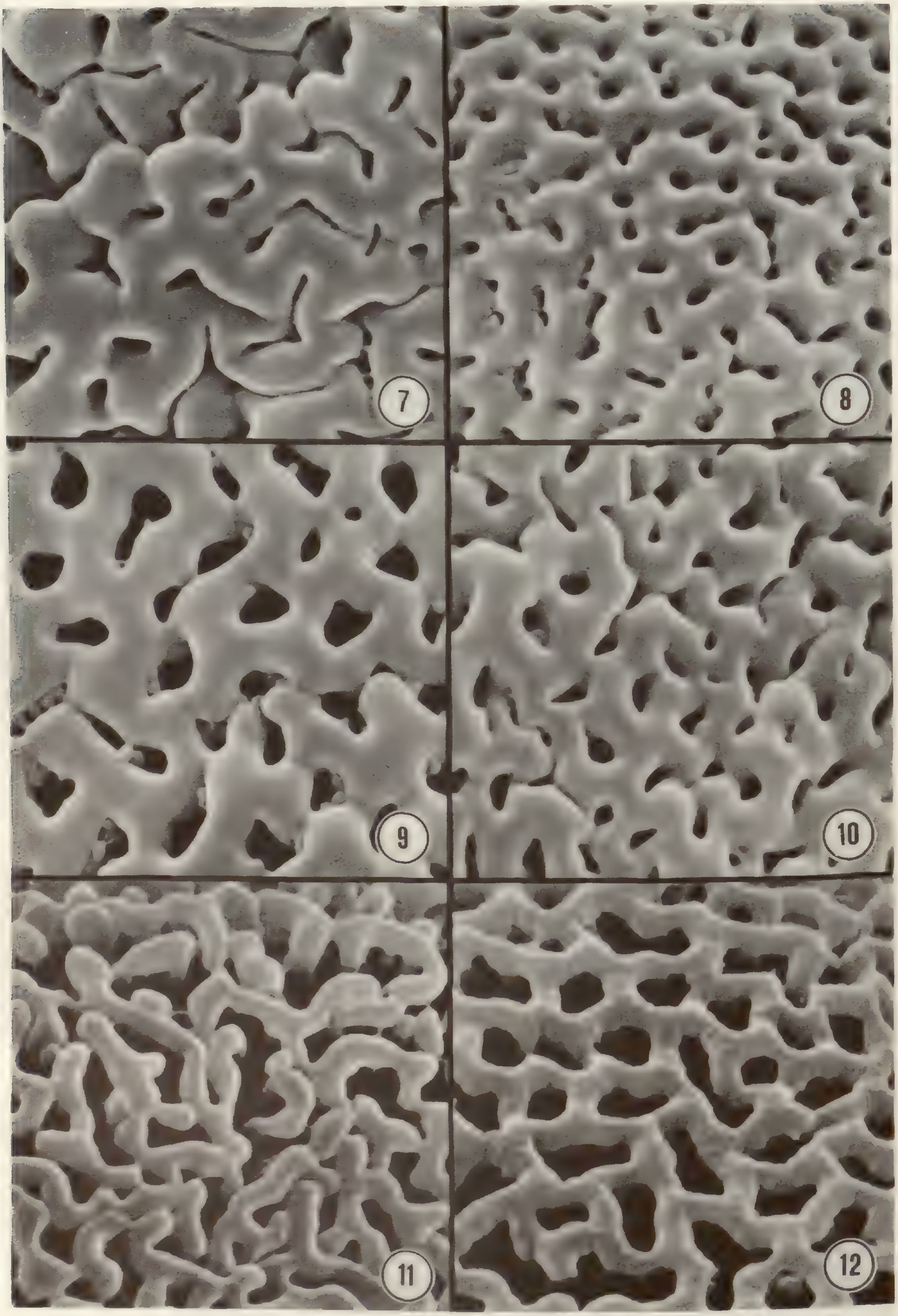
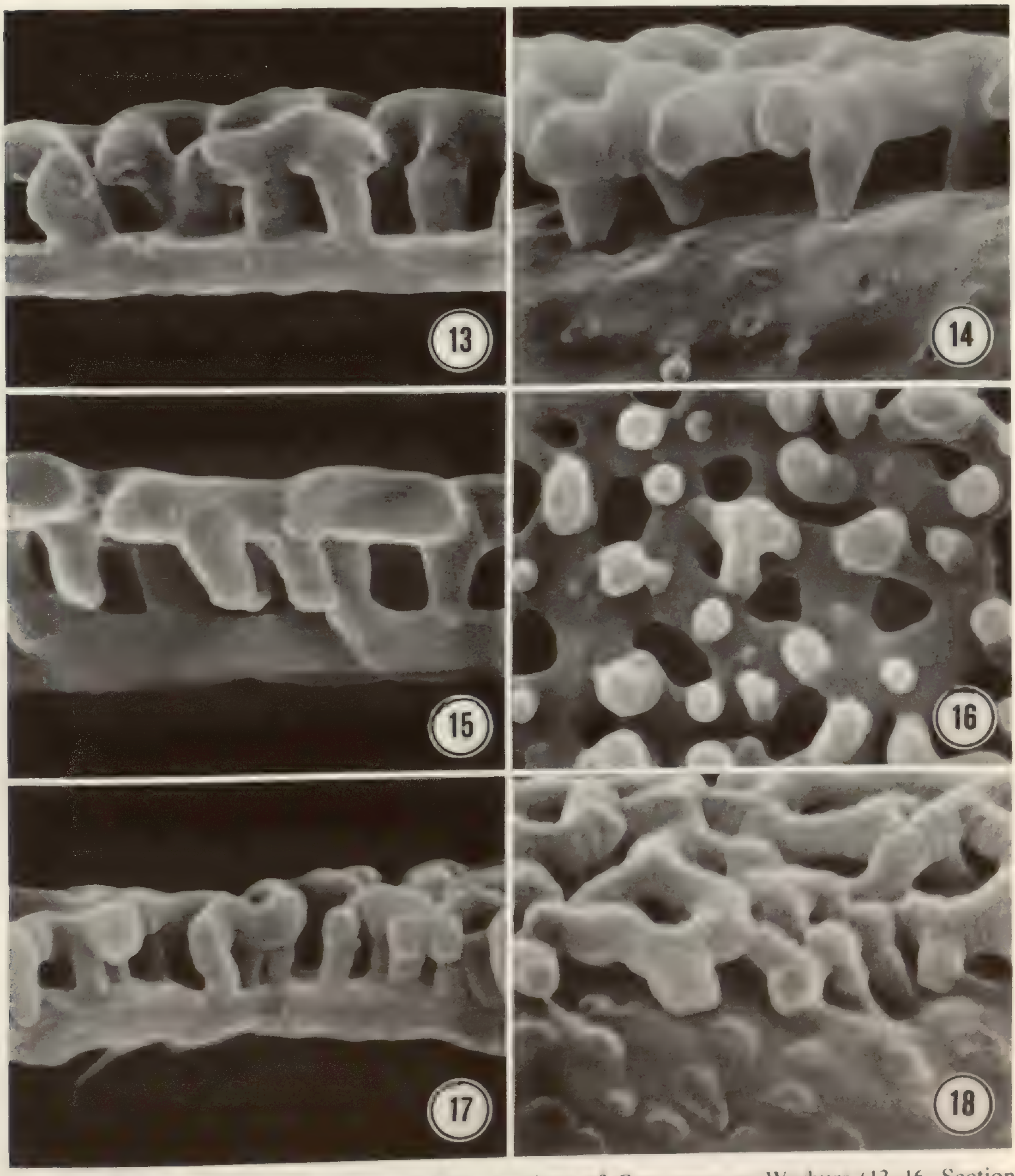
Figures 1–6. Whole pollen grains of *Compsoneura* Warburg (1–4, Section *Compsoneura*; 5–6, Section *Coniostele* Warburg).—1–2. *C. capitellata* (A. DC.) Warburg (*Klug 2130*, 1, P-1956; 2, P-895), 1, apertural side, 2, nonapertural side; both ×2,500.—3. *C. debilis* (A. DC.) Warburg (*Ducke 36*, P-2707); ×2,500.—4. *C. sprucei* (A. DC.) Warburg (*J. D. Smith 5256*, P-1948); ×2,100.—5. *C. excelsa* A. C. Smith (*Skutch 2791*, P-1950); ×3,000.—6. *C. ulei* Warburg (*Prance et al. 8562*, P-1954); ×2,200.

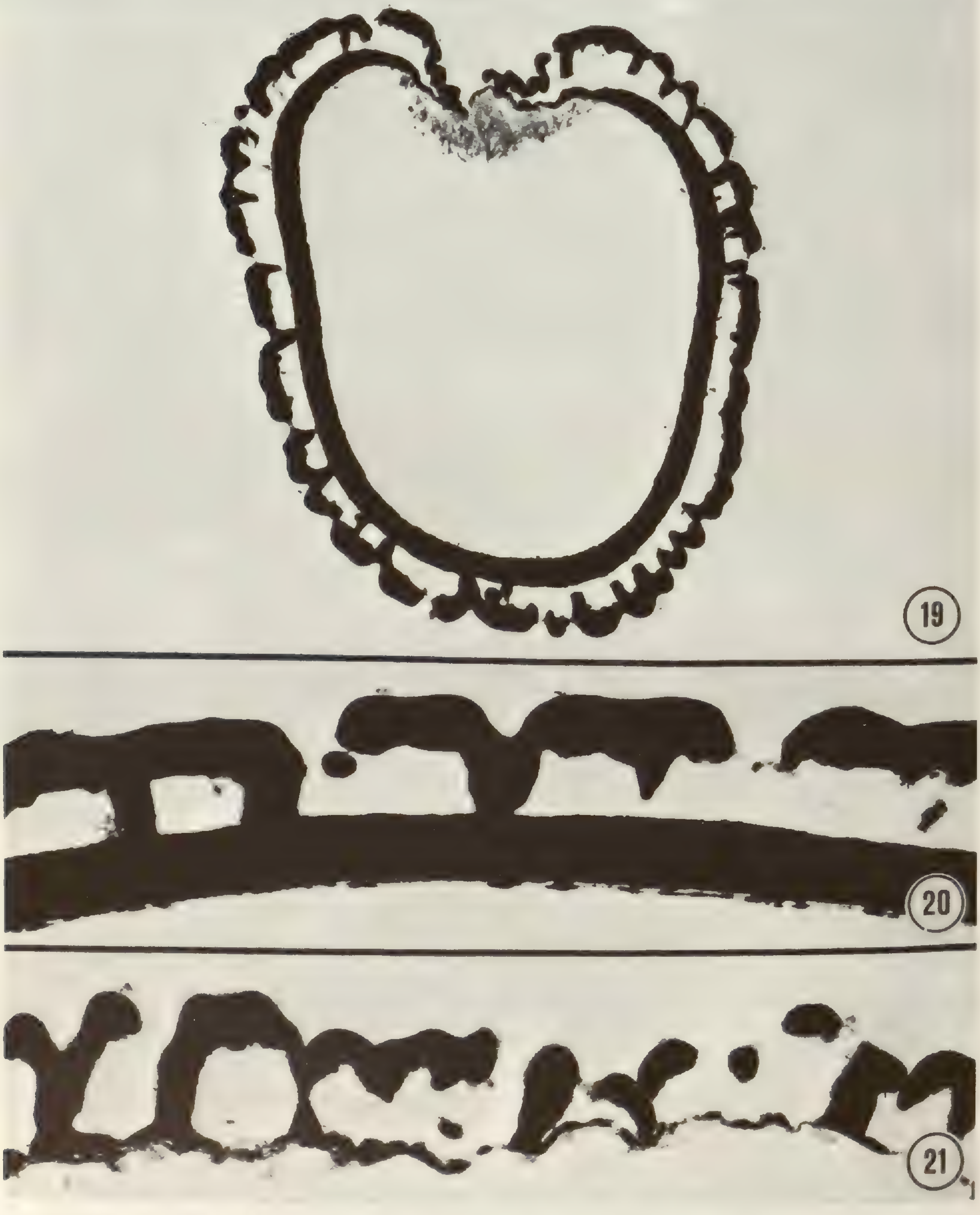


FIGURES 7–12. Exine surface of *Compsoneura* Warburg (7–10. Section *Compsoneura*; 11–12. Section *Coniostele* Warburg).—7. *C. capitellata* (A. DC.) Warburg (*Klug 2130*, P-895).—8. *C. racemosa* Ducke (*Krukoff 8754*, P-2708).—9. *C. sprucei* (A. DC.) Warburg (*J. D. Smith 5256*, P. 1948).—10. *C. debilis* (A. DC.) Warburg (*Ducke 36*, P-2707).—11. *C. excelsa* A. C. Smith (*Skutch 2791*, P-1950).—12. *C. ulei* Warburg (*Prance et al. 8562*, P-1954). All ×12,000.

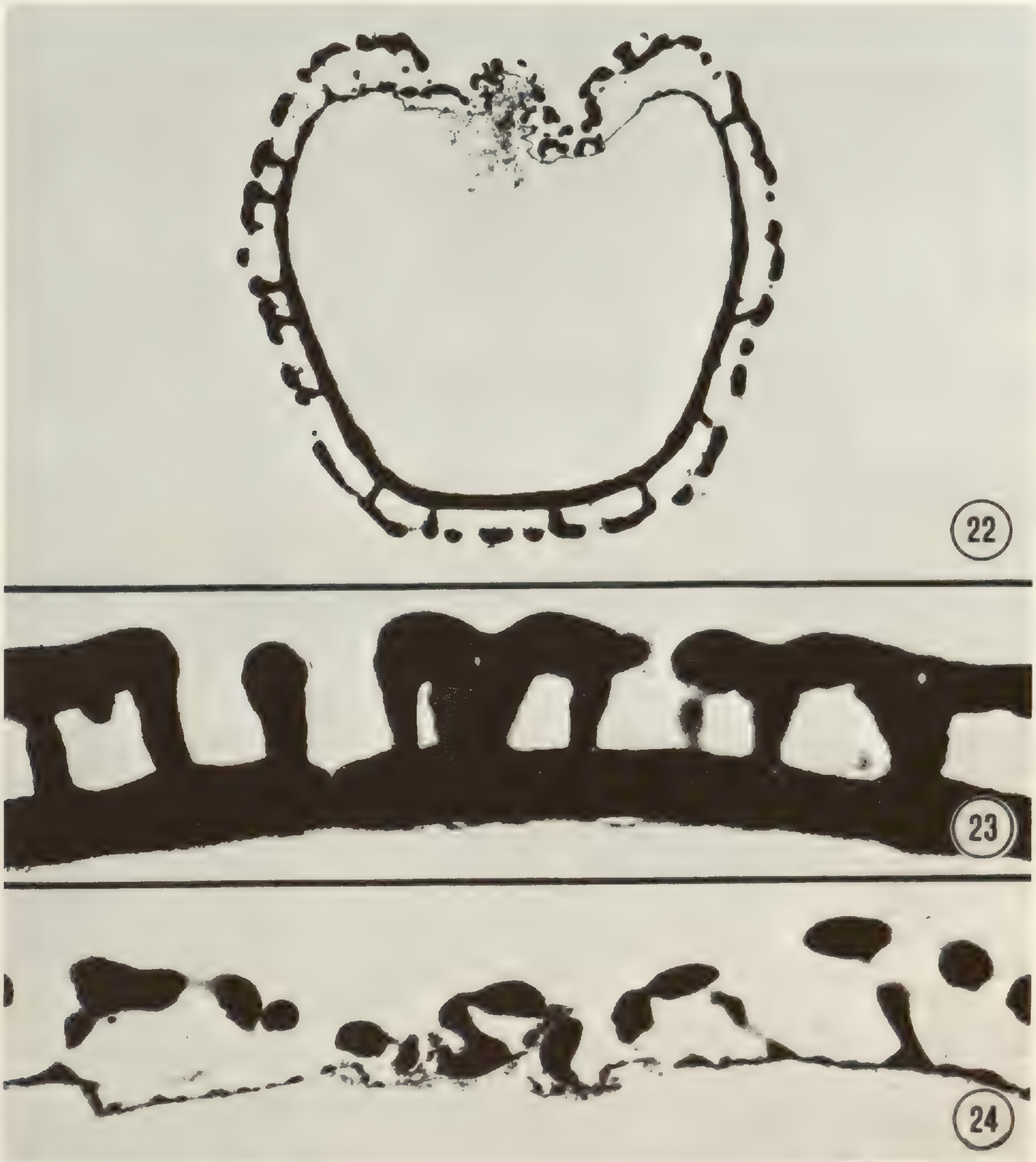


FIGURES 13–18. SEM nonapertural exine sections of *Compsoneura* Warburg (13–16, Section *Compsoneura*; 17–18, Section *Coniostele* Warburg).—13. *C. debilis* (A. DC.) Warburg (*Ducke 36*, P-2707).—14. *C. capitellata* (A. DC.) Warburg (*Klug 2130*, P-895), note circular depressions left on surface of nexine by separation of weakly attached columellae.—15–16. *C. sprucei* (A. DC.) Warburg (*J. D. Smith 5256*, P-1948), 15, cross-section, note columellae pendulous from inner surface of tectum, 16, tangential section through interstitium looking at inner surface of tectum, note granules on inner surface of tectum mixed in with columellae.—17. *C. excelsa* A. C. Smith (*Skutch 2791*, P-1950).—18. *C. ulei* Warburg (*Prance et al. 8562*, P-1954), note circular depressions in surface of nexine where columellae were attached to nexine. All ×16,000.

Specimens Examined.—*Compsoneura capitellata* (A. DC.) Warburg, *Klug 2130* (GH), P-895 (SEM, SEM-X, TEM), (K), P-1956 (SEM); *Ducke I.A.N. 143* (K), P-1953. *C. debilis* (A. DC.) Warburg, *Ducke 36* (A), P-894, (K), P-1951 (SEM, TEM), (S), P-2707 (SEM, SEM-X). *C. excelsa* A. C. Smith, *Haught 1733* (A), P-1134 (SEM). *C. racemosa* Ducke, *Krukoff 8754* (A), P-1135, (K), P-1952 (SEM), (S), P-2708 (SEM). *C. sprucei* (A. DC.) Warburg, *Bartlett 11330* (A), P-892; *Bangham 357* (A), P-893; *J. Skutch 2791* (GH), P-1133 (SEM), (K), P-1950 (SEM, SEM-X). *C. mutisii* A. C. Smith, *Haught*



FIGURES 19–21. TEM exine sections of *Compsoneura capitellata* (A. DC.) Warburg (*Klug 2130*, P-895).—19. Whole grain exine section, showing aperture at top and partly acetolysis-resistant intine beneath, ×4,600.—20. Nonapertural exine section, showing average, essentially solid nexine, average to moderately thick columellate interstitium, and average tectum, ×15,000.—21. Apertural exine section, showing extremely to very thin nexine and greatly reduced and much disorganized sexine, ×18,000.



FIGURES 22–24. TEM exine sections of *Compsoneura sprucei* (A. DC.) Warburg (*J. D. Smith 5256*, P-1948).—22. Whole grain exine section, showing aperture at top, ×3,500.—23. Nonapertural exine section, showing average, essentially solid nexine, average to moderately thick columellate interstitium, and average tectum, ×18,000.—24. Apertural exine section, showing extremely to very thin nexine and greatly reduced and much disorganized sexine, ×13,000.

D. Smith 5256 (K), P-1948 (SEM, SEM-X, TEM); *Gentle 2640* (K), P-1949. *C. ulei* Warburg, *Prance et al. 8562* (GH), P-1136, (K), P-1954 (SEM, SEM-X); *Prance et al. 8979* (K), P-1955.

Virola Aubl. (Figs. 25–96)

Pollen.—Apertures sulcate and generally sharply delimited externally, sometimes more or less sulcoidate and less evident externally. Shape usually boat-shaped, less commonly more or less globose-spherical, sometimes rectangular or triangular in outline with a straight apertural face and a markedly convex non-

apertural face. Polarity heteropolar. Symmetry usually bilateral, less commonly isobilateral. Size medium-sized to small (mean 27 μm, range 22–35 μm). Pollen-Unit monads. Exine Sculpturing reticuloid to reticulate, sometimes with banded, beaded, or granulate-beaded muri and occasionally with evident, free-standing columellae visible through the lumina of the reticulum. Exine Structure columellate (columellae frequently weakly attached to the nexine), tectate-perforate to semitectate; nonapertural exine about 1.35 μm thick, with a generally very thin (about 13% of total exine thickness on the average), although sometimes extremely thin or moderately thin, partially finely lamellate or essentially solid nexine, a moderately thick (about 46% of total exine thickness on the average) interstitium, and an average to moderately thick (about 41% of total exine thickness on the average) tectum, sexine usually with conspicuous, small, spherical, intra-exinous cavities; apertural exine with an extremely to very thin nexine and a reduced and much disorganized sexine. Exine Stratification wholly ektexinous; endexine none.

Specimens Examined.—Virola albidiflora Ducke, *Schultes & Cabrera 13974* (A), P-1152; *Forero et al. 6370* (S), P-2716; *Krukoff 8103* (S), P-2717. *V. calophylla* Warburg, *Krukoff 4713* (A), P-914,

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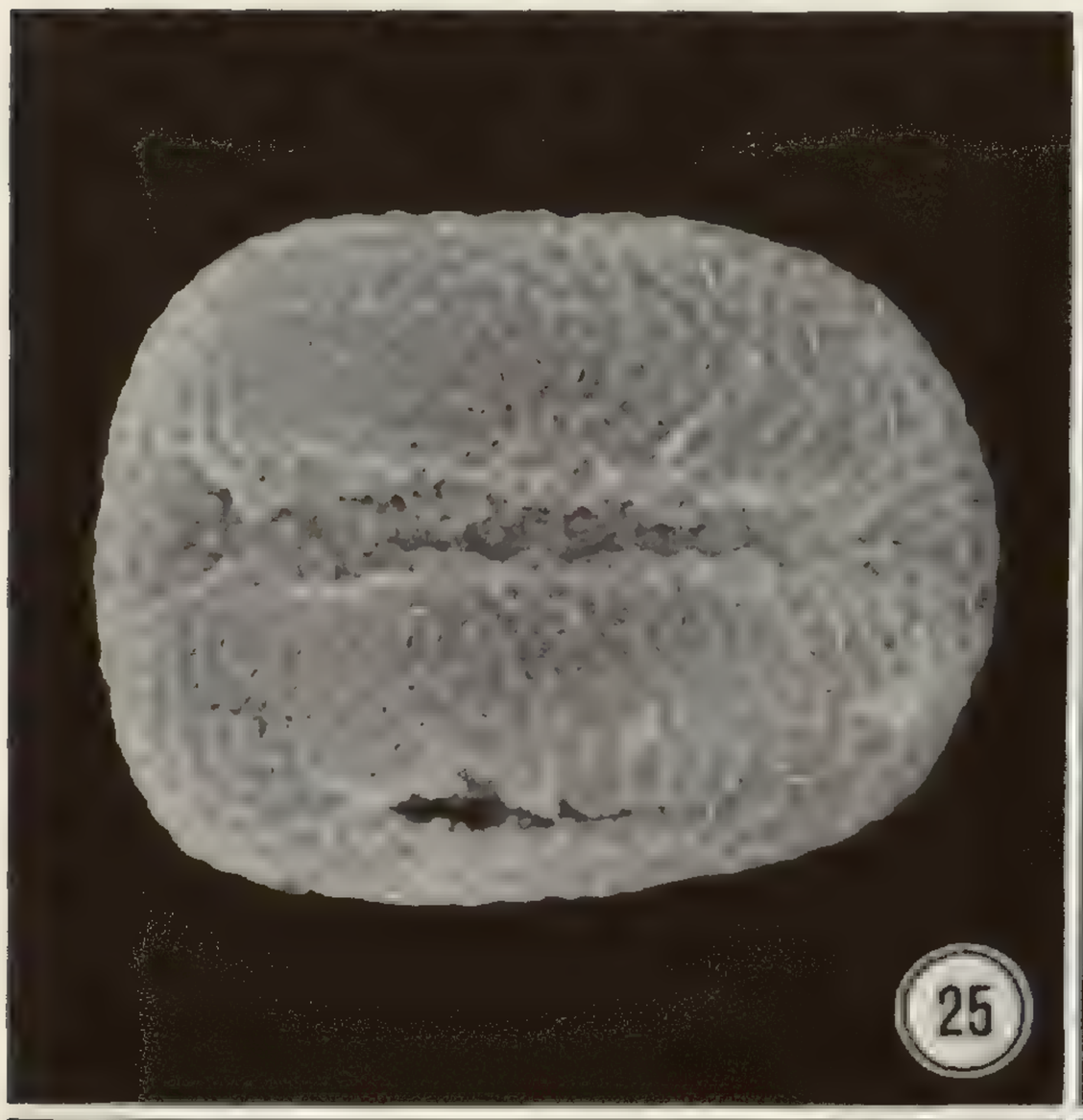
FIGURES 25–30. Whole pollen grains and apertural surface views of Type I pollen of *Virola* Aubl.—25. *V. calophylla* Warburg (*Krukoff 4713*, P-1995); ×2,200.—26. *V. elongata* (Benth.) Warburg (*Prance et al. 14081*, P-2010); ×2,500.—27, 29. *V. cuspidata* (Benth.) Warburg (27, *Ducke 24467*, P-1991; 29, *Prance et al. 15120*, P-1990), 29, apertural surface view; 27, ×2,000, 29, ×15,000.—28, 30. *V. duckei* A. C. Smith (28, *Wurdack 2259*, P-2719; 30, *Froes 21248*, P-1999), 30, apertural surface view; 28, ×3,000, 30, ×8,000.

FIGURES 31–36. Whole pollen grains of Type II pollen of *Virola* Aubl.—31. *V. minutiflora* Ducke (*Ducke 251*, P-2726); ×3,400.—32. *V. weberbaueri* Markgraf (*Tessmann 4339*, P-2734); ×2,800.—33. *V. malmei* A. C. Smith (*Malme 2033b*, P-2724); ×2,200.—34. *V. surinamensis* (Rol.) Warburg (*Plantae Surinamenses 700*, P-2002); ×2,000.—35. *V. calophylloidea* Markgraf (*Maguire et al. 56666*, P-1997); ×2,800.—36. *V. multinervia* Ducke (*Maas et al. P12796*, P-2728); ×2,000.

FIGURES 37–42. Whole pollen grains and apertural surface views of Type III pollen of *Virola* Aubl.—37, 39. *V. koschnyi* Warburg (*Peck 373*, P-1985), 39, apertural surface view; 37, ×2,200, 39, ×16,000.—38, 40. *V. multiflora* (Standl.) A. C. Smith (38, *Schipp 858*, P-1149; 40, *Schipp 279*, P-1986), 40, apertural surface view; 38, ×1,800, 40, ×7,000.—41. *V. melinonii* (Benoist) A. C. Smith (*Pires et al. 50526*, P-2725); ×2,000.—42. *V. venosa* (Benth.) Warburg (*Pires et al. 50550*, P-2005), note the numerous free-standing columellae visible through lumina of the reticulum; ×2,000.

FIGURES 43–49. Exine surface of Type I pollen of *Virola* Aubl.—43. *V. calophylla* Warburg (*Krukoff 4713*, P-1995); ×16,000.—44. *V. macrocarpa* A. C. Smith (*Cuatrecasas 17540*, P-1158); ×16,000.—45. *V. peruviana* (A. DC.) Warburg (*Schultes 6031*, P-2013); ×12,000.—46. *V. mollissima* (A. DC.) Warburg (*Klug 3128*, P-913); ×12,000.—47. *V. elongata* (Benth.) Warburg (*Prance et al. 14081*, P-2010); ×16,000.—48. *V. loretensis* A. C. Smith (*Klug 2822*, P-2012); ×12,000.—49. *V. duckei* A. C. Smith (*Wurdack 2259*, P-2719); ×16,000.

FIGURES 50–57. Exine surface of Type II pollen of *Virola* Aubl.—50. *V. glaziovii* Warburg (*Maguire et al. 56267*, P-2003), note very faintly banded muri; ×12,000.—51. *V. malmei* A. C. Smith (*Malme 2033b*, P-2724), note faintly banded muri; ×12,000.—52. *V. carinata* (Benth.) Warburg (*Ule 7988*; P-2007), note faintly banded muri; ×24,000.—53. *V. multinervia* Ducke (*Maas et al. P12796*, P-2728), note banded muri; ×16,000.—54. *V. calophylloidea* Markgraf (*Maguire et al. 56666*, P-1997), note distinctly banded muri; ×16,000.—55, 57. *V. weberbaueri* Markgraf (*Tessmann 4339*, P-2734), note coarsely granulate-banded muri; 55, ×12,000, 57, ×24,000.—56. *V. pavonis* (A. DC.) A. C. Smith (*Ducke 259*, P-1160), note coarsely granulate-banded muri; ×12,000.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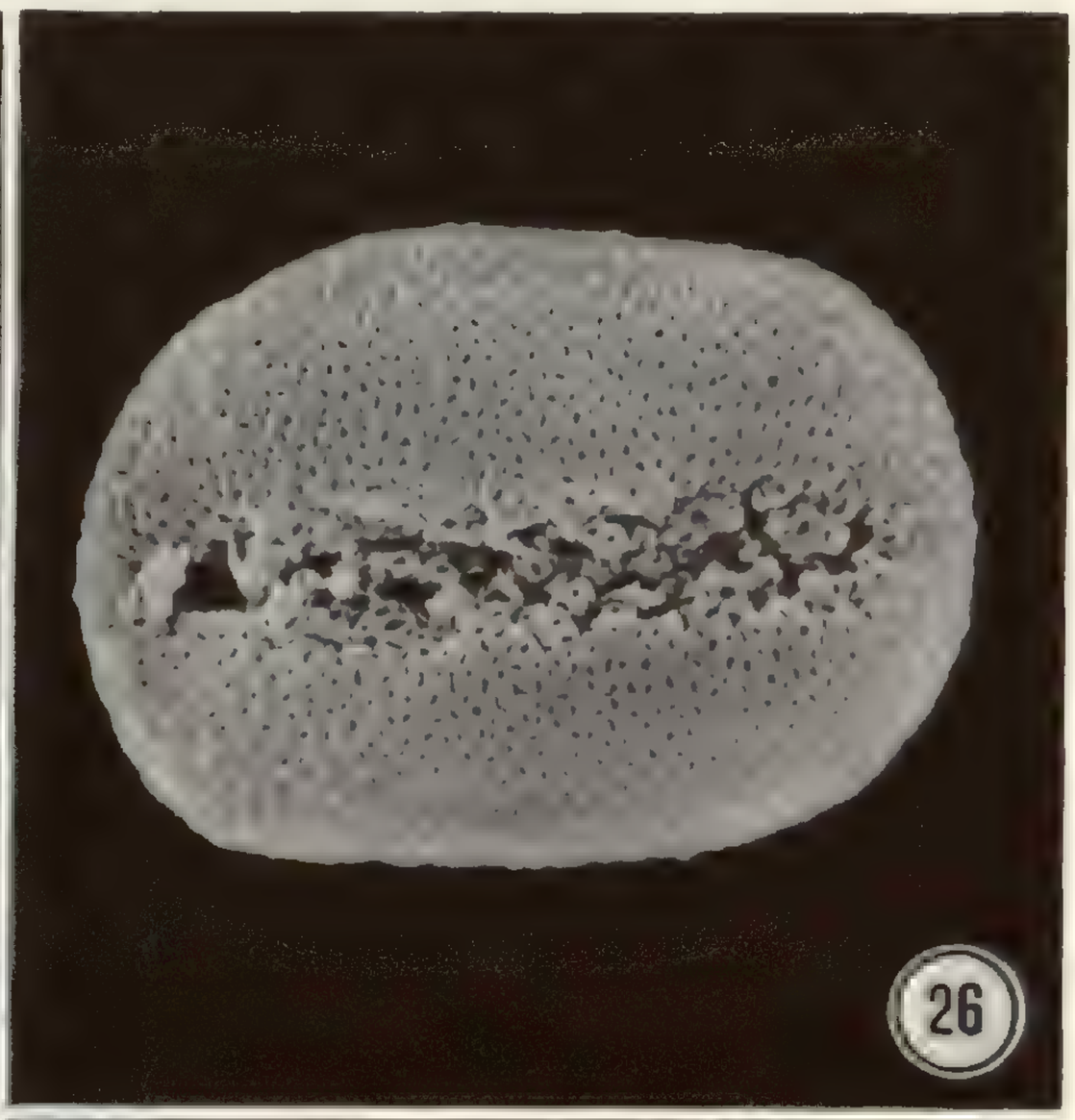
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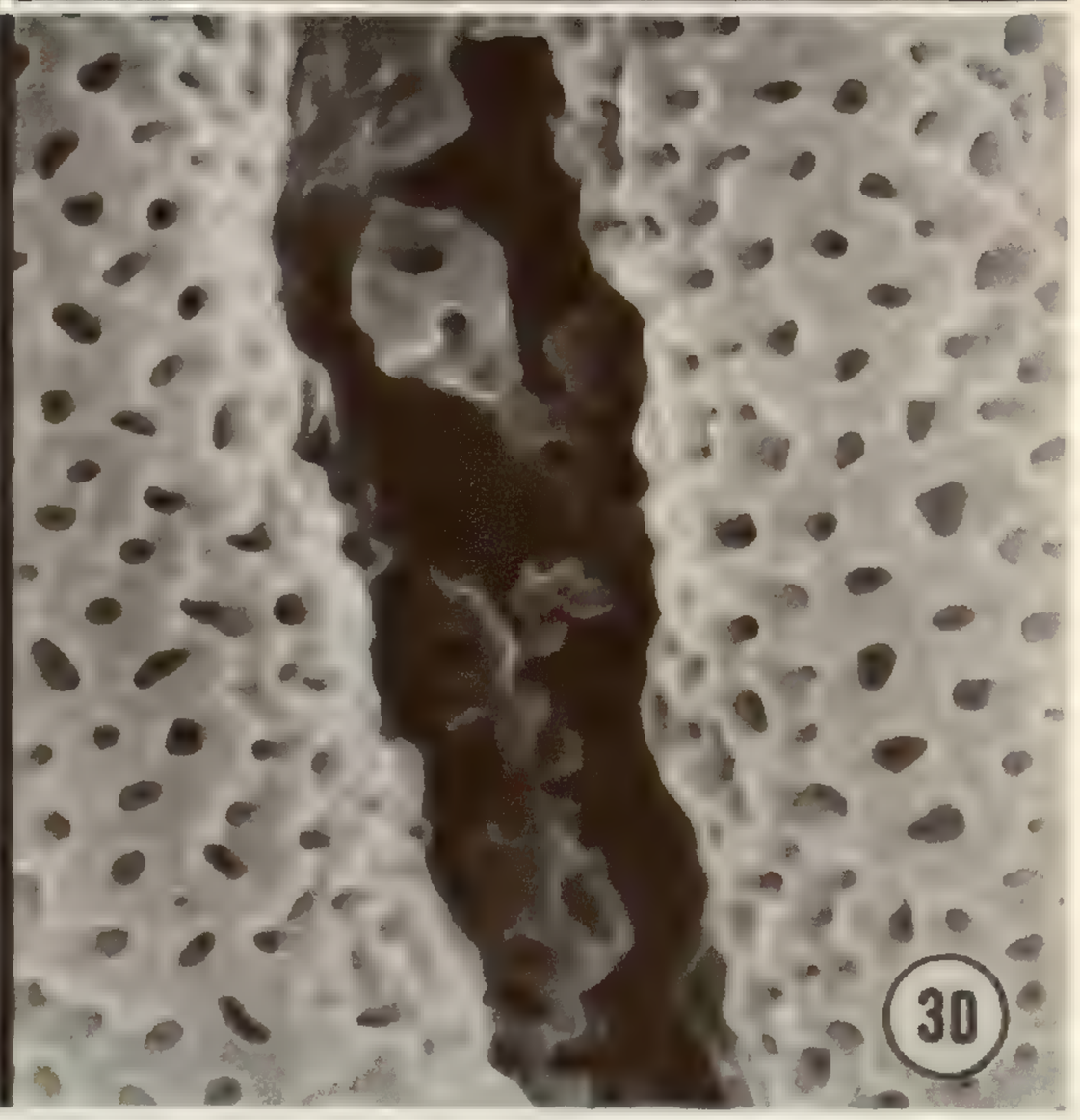
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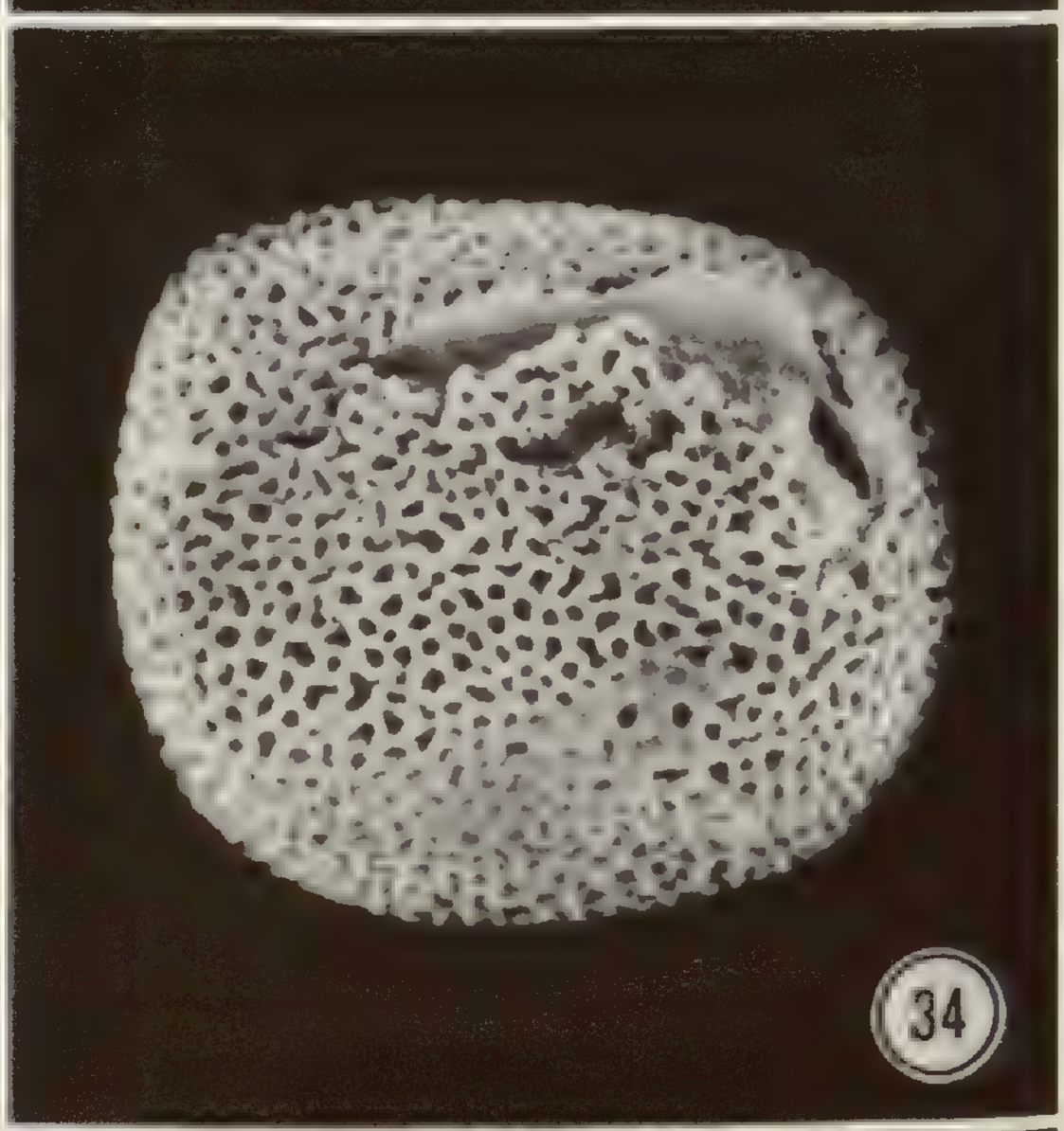
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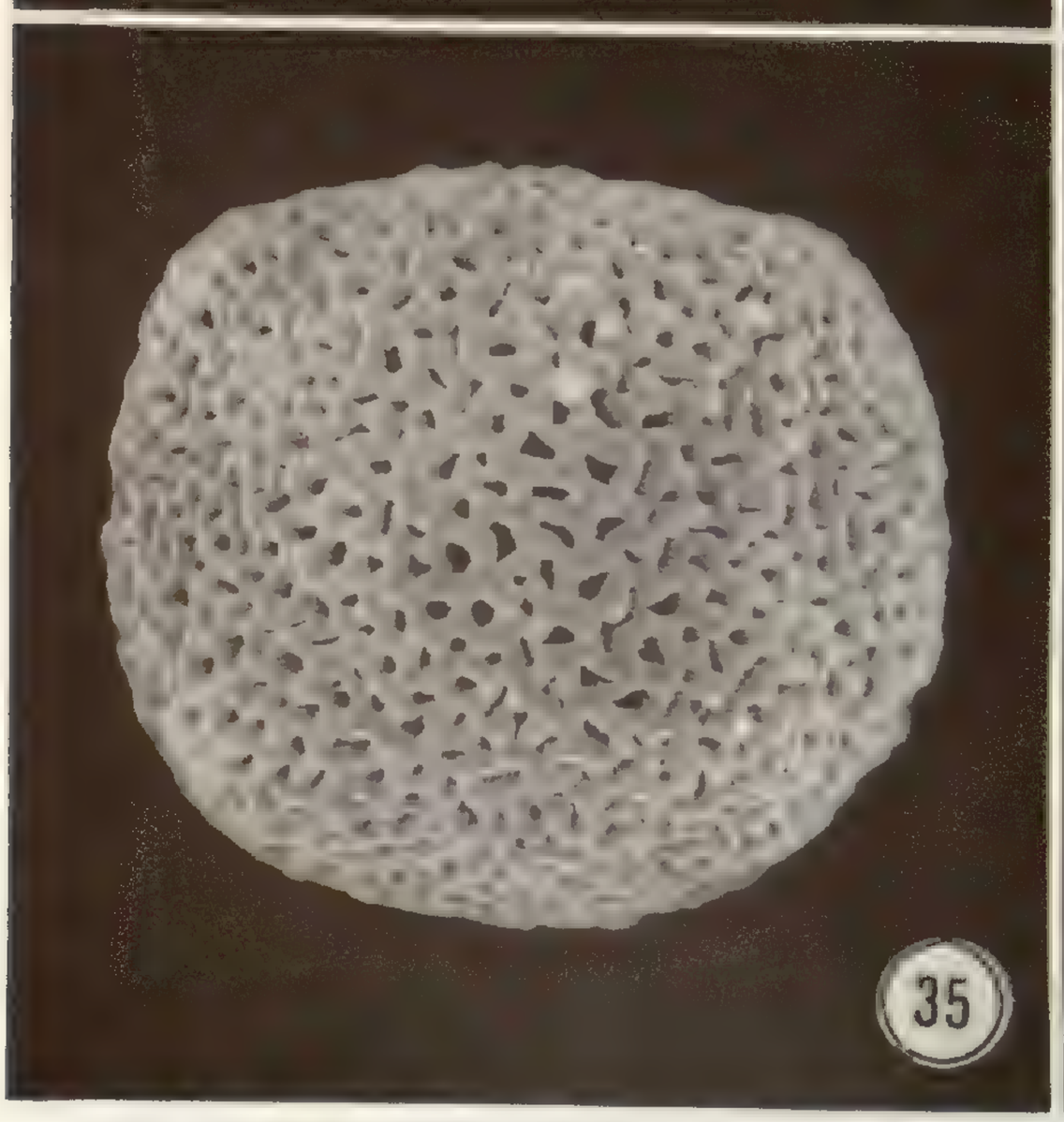
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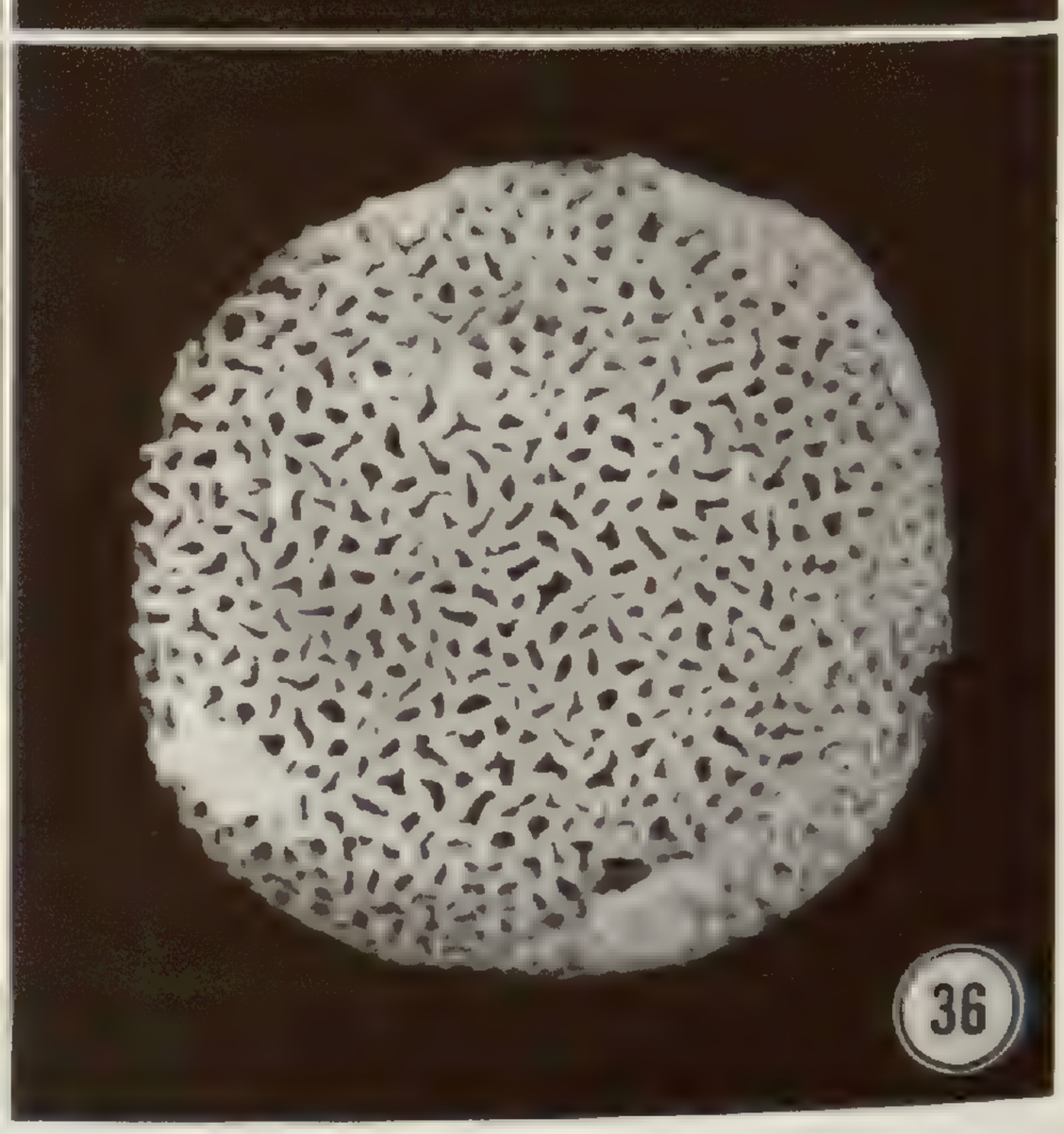
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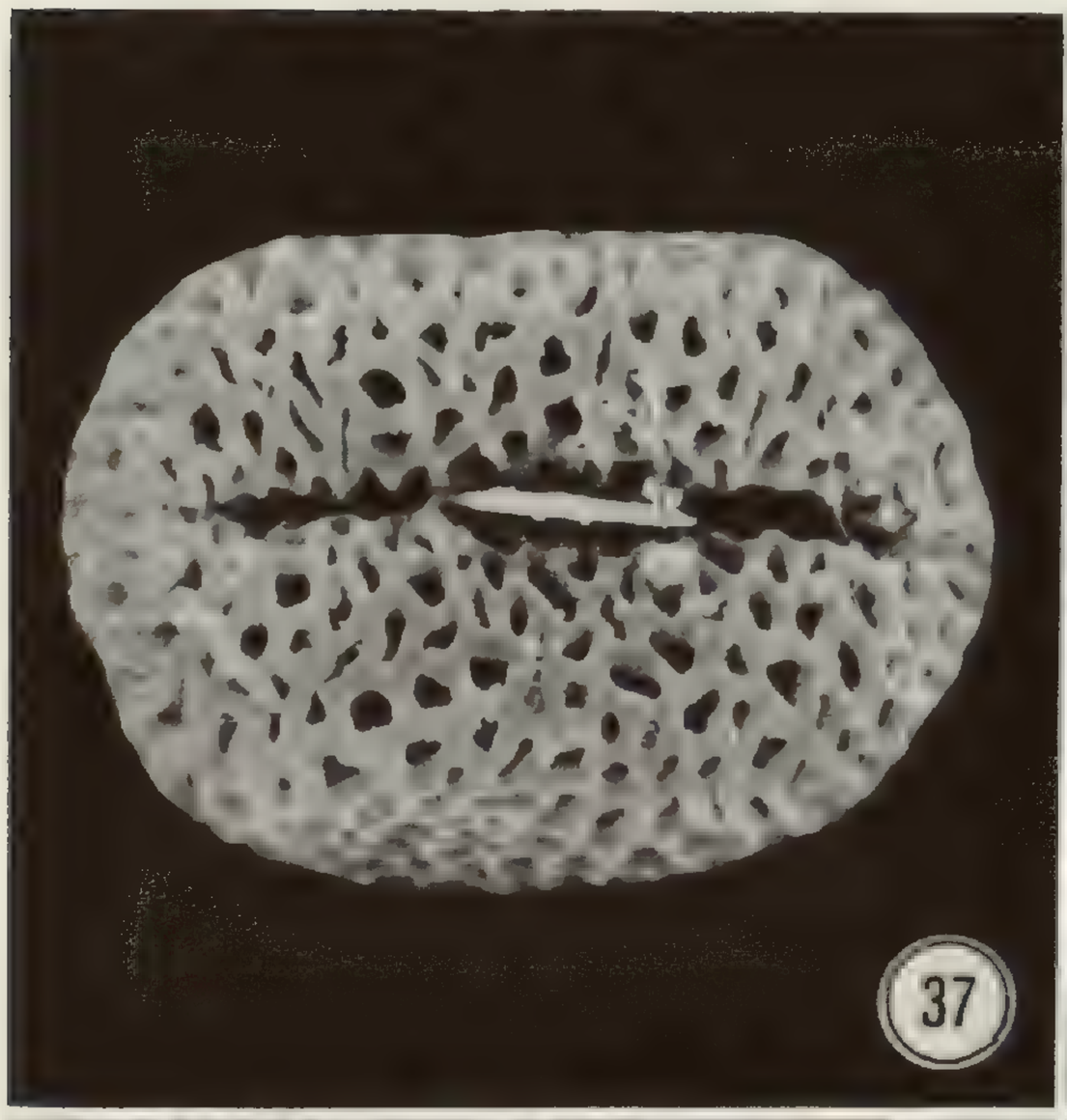
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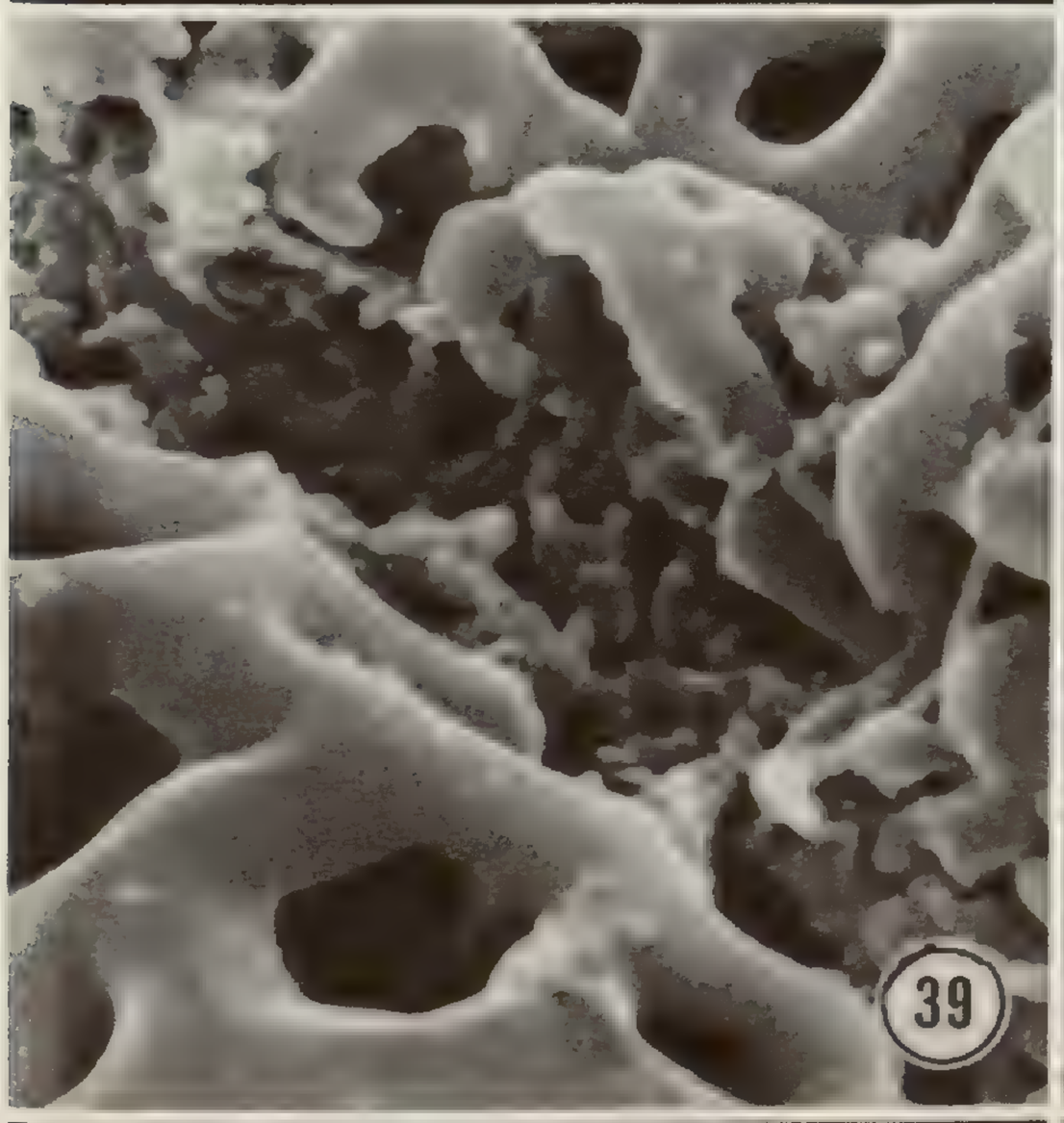
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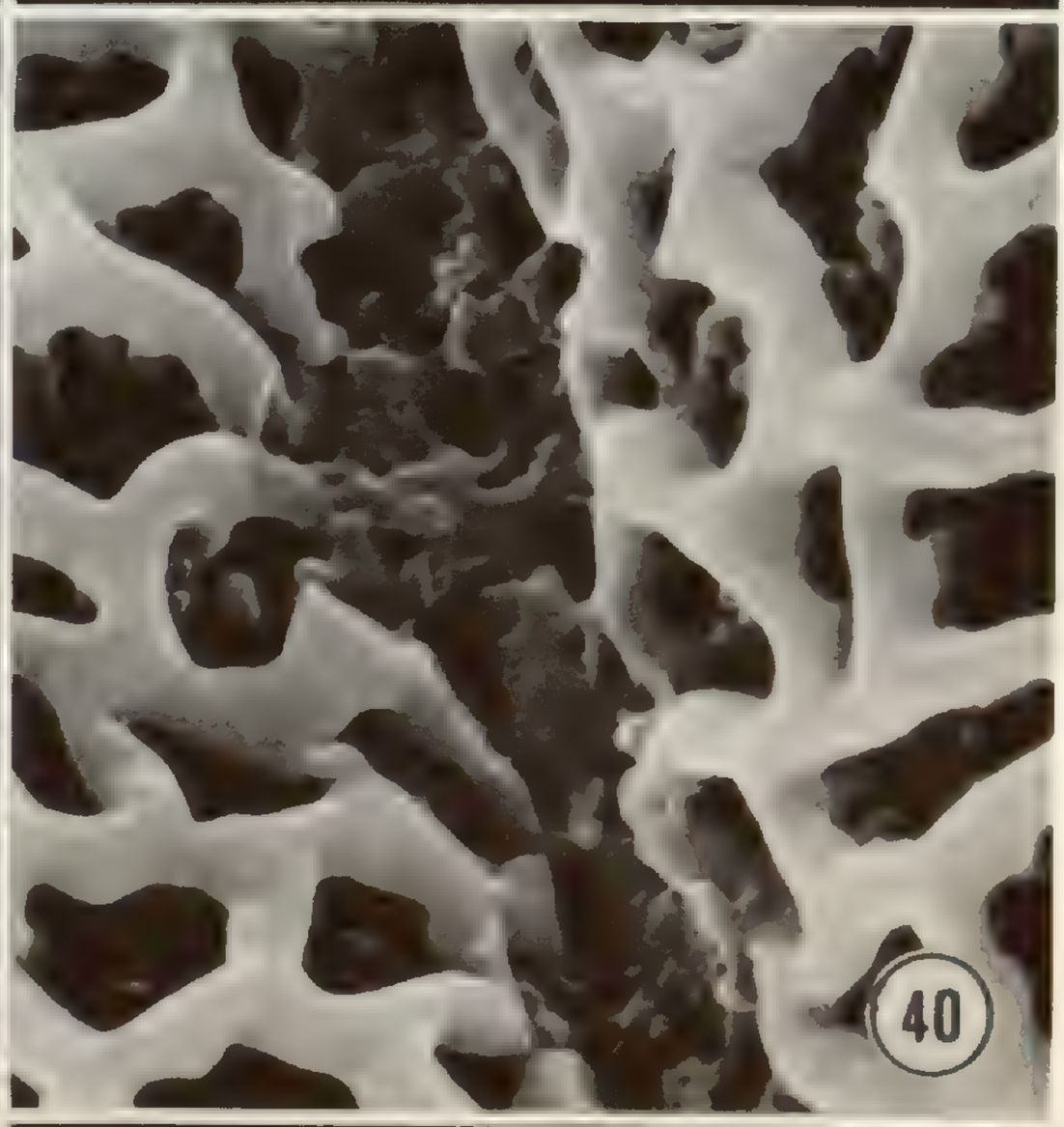
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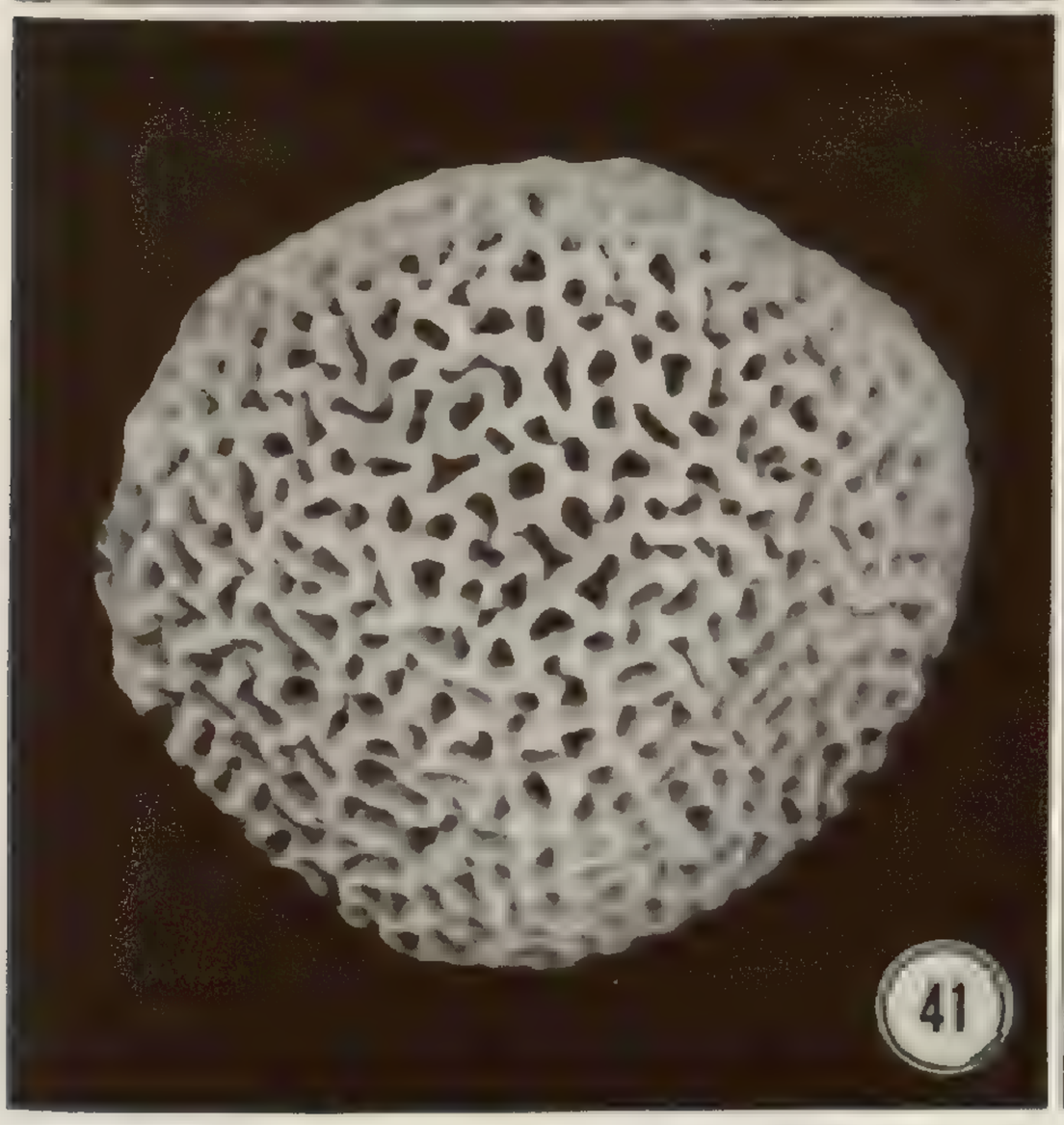
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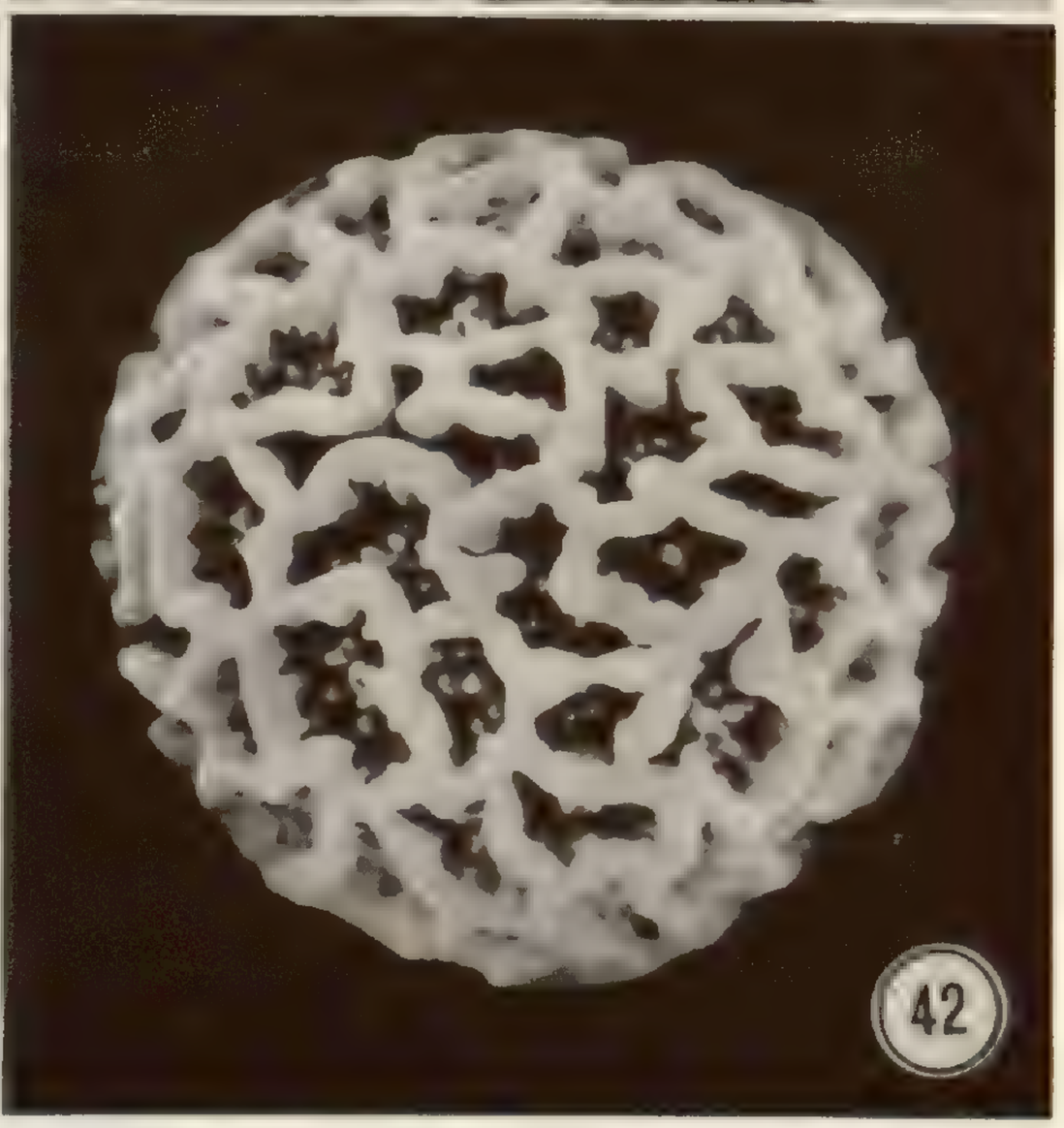
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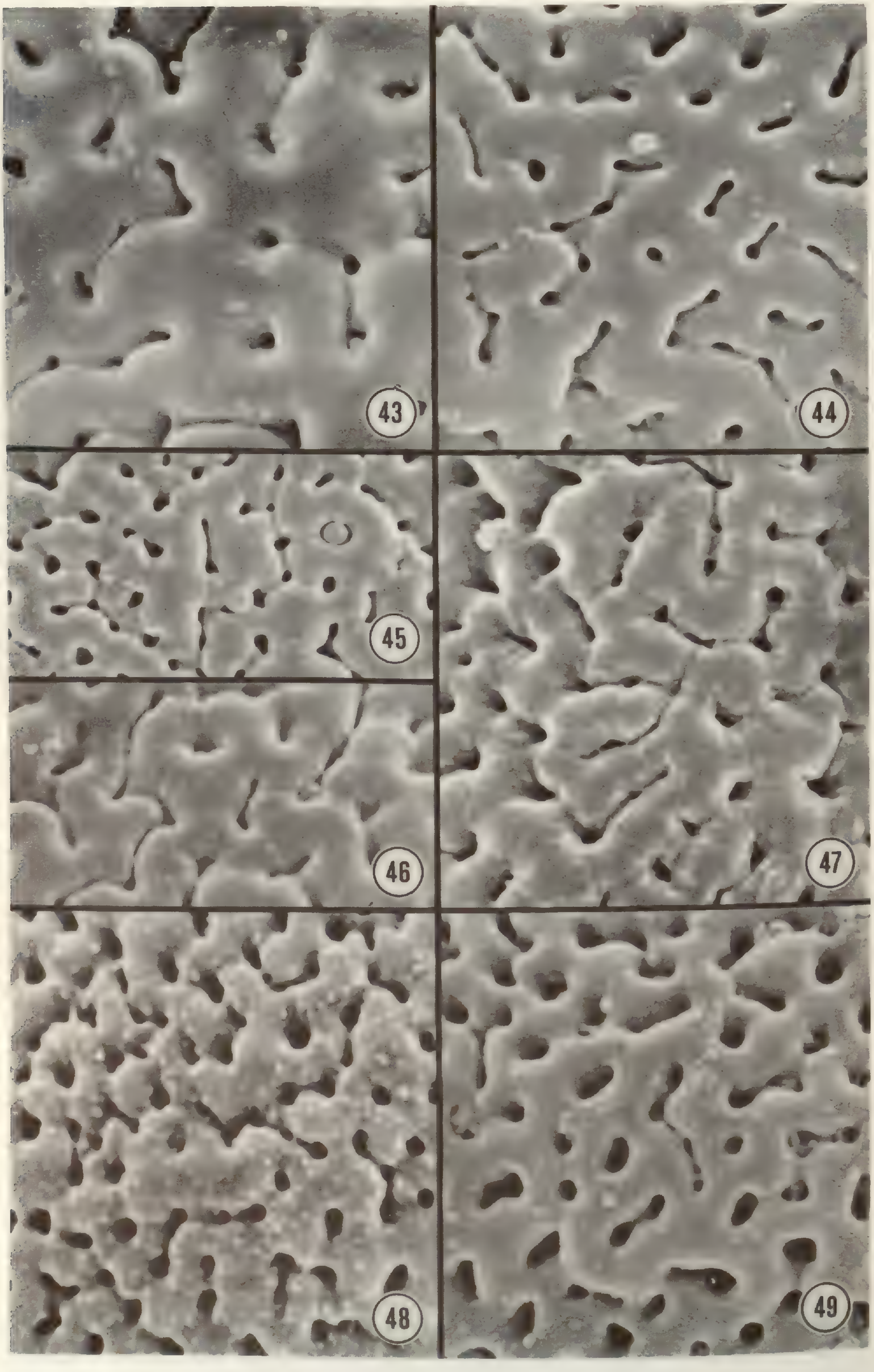
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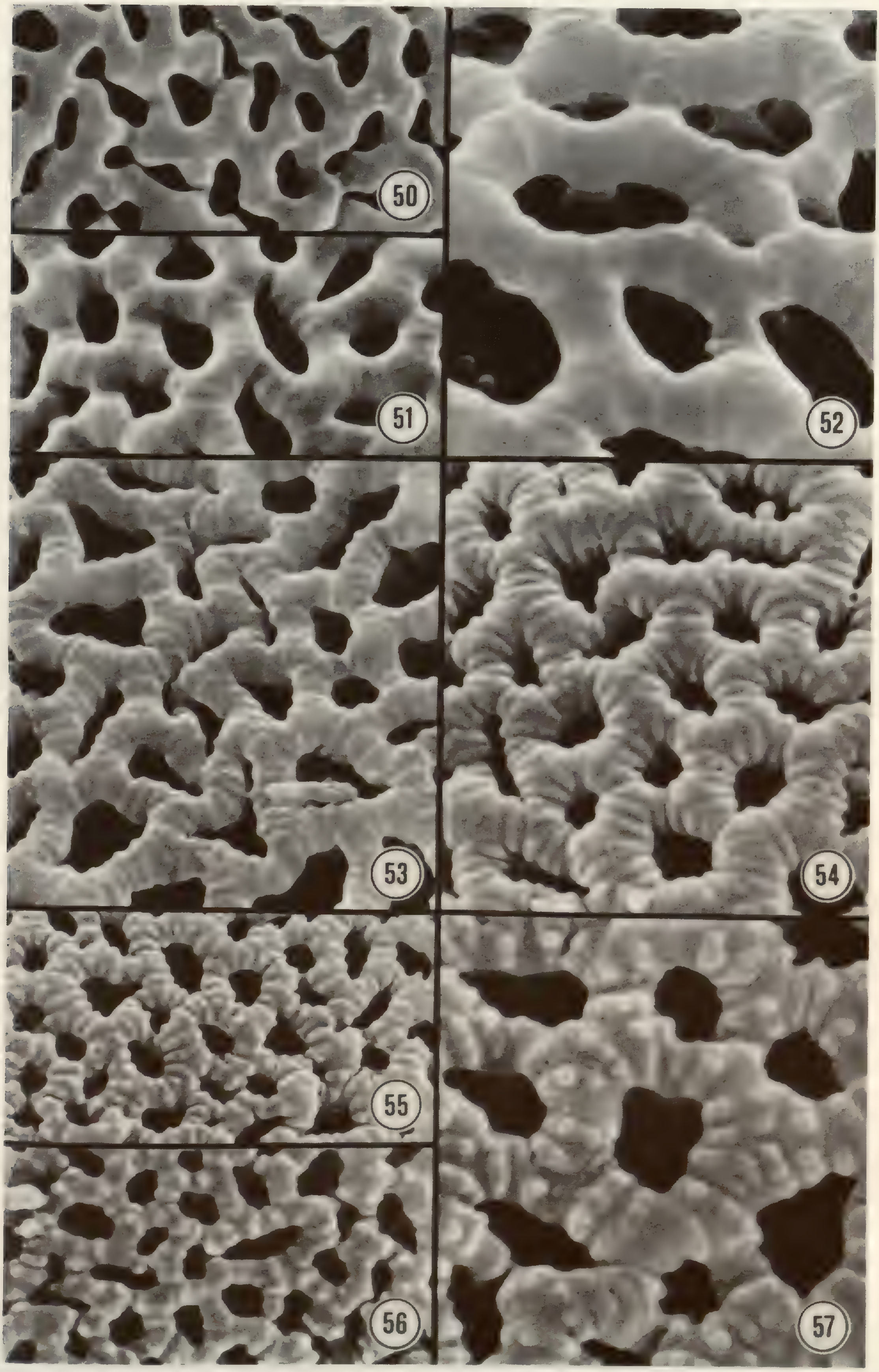
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(K), P-1995 (SEM); *Froes 21222* (K), P-1994 (SEM). *V. calophylloidea* Markgraf, *Ducke 20* (A), P-1153, (S), P-2718; *Maguire et al. 56666* (K), P-1997 (SEM). *V. carinata* (Benth.) Warburg, *Froes 21172* (GH), P-912; *Ule 7988* (K), P-2007 (SEM, TEM); *Schultes & Black 8352* (K), P-2015 (SEM, TEM). *V. cuspidata* (Benth.) Warburg, *Ducke 254* (A), P-909; *Prance et al. 15120* (K), P-1990 (SEM); *Ducke 24467* (K), P-1991 (SEM). *V. divergens* Ducke, *Krukoff 1120* (A), P-1154 (SEM), (K), P-1987 (SEM, SEM-X, TEM); *Ducke 174* (K), P-1988. *V. duckei* A. C. Smith, *Froes 21248* (K), P-1999 (SEM); *Wurdack 2259* (S), P-2719 (SEM). *V. elongata* (Benth.) Warburg, *Prance et al. 3259* (GH), P-1156; *Klug 2944* (A), P-1164; *A. C. Smith 2524* (K), P-1993 (SEM); *Prance et al. 14081* (K), P-2010 (SEM, SEM-X, TEM). *V. flexuosa* A. C. Smith, *Tessmann 3207* (S), P-2720 (SEM, TEM). *V. gardneri* (A. DC.) Warburg, *Ducke 25105* (S), P-2721. *V. glaziovii* Warburg, *Maguire et al. 56267* (K), P-2003 (SEM, SEM-X). *V. guatemalensis* (Hemsl.) Warburg, *Steyermark 47624* (A), P-1148 (SEM). *V. koschnyi* Warburg, *Skutch 4260* (A), P-908 (SEM), (S), P-2722; *Peck 373* (K), P-1985 (SEM, SEM-X, TEM). *V. loretensis* A. C. Smith, *Klug 2822* (K), P-2012 (SEM, TEM). *V. macrocarpa* A. C. Smith, *Cuatrecasas 17540* (A), P-1158 (SEM, TEM). *V. malmei* A. C. Smith, *Malme 2033b* (S), P-2724 (SEM). *V. melinonii* (Benoist) A. C. Smith, *Ducke 1268* (A), P-1159; *Pires et al. 50526* (S), P-2725 (SEM). *V. minutiflora* Ducke, *Ducke 251* (S), P-2726 (SEM). *V. mollissima* (A. DC.) Warburg, *Klug 3128* (A), P-913 (SEM), (S), P-2727 (SEM, SEM-X). *V. multiflora* (Standl.) A. C. Smith, *Schipp 858* (GH), P-1149 (SEM); *Schipp 279* (K), P-1986 (SEM, TEM). *V. multinervia* Ducke, *Ducke 24556* (K), P-1998; *Maas et al. P12796* (S), P-2728 (SEM). *V. nobilis* A. C. Smith, *Allen 5774* (GH), P-1150 (SEM). *V. officinalis* Warburg, *Martius 183* (L), P-2831 (SEM). *V. oleifera* (Schott) A. C. Smith, *Glaziou 12140* (K), P-2000 (SEM, SEM-X). *V. pavonis* (A. DC.) A. C. Smith, *Ducke 259* (A), P-1160 (SEM); *Ruiz 61* (K), P-2014 (SEM); *Klug 3085* (K), P-2016. *V. peruviana* (A. DC.) Warburg, *Wurdack 2272* (GH), P-1161; *Ducke 24552* (K), P-1996 (SEM); *Schultes 6031* (K), P-2013 (SEM, SEM-X, TEM). *V. sebifera* Aubl., *Skutch 3118* (A), P-1151 (SEM), (K), P-1984; *Krukoff 11644* (K), P-1989 (SEM). *V. sessilis* (A. DC.) Warburg, *Malme 2007c* (S), P-2729 (SEM, TEM); *Malme 2007b* (S), P-2730 (SEM, TEM). *V. subsessilis* (Benth.) Warburg, *Irwin et al. 21508* (GH), P-1163; *Prance & Silva 58503* (S), P-2732 (SEM). *V. surinamensis* (Rol.) Warburg, *Eggers s.n.* (GH) P-910; *Sandwith 477* (K), P-2001; *Plantae Surinamenses 700* (K), P-2002 (SEM). *V. venosa* (Benth.) Warburg, *Herb. Acad. Rhenotraiect, Arbor No. 1336* (A), P-1165; *Pires et al. 50550* (K), P-2005 (SEM); *Prance et al. 6749* (S), P-2733. *V. weberbaueri* Markgraf, *Tessmann 4339* (S), P-2734 (SEM, SEM-X, TEM).

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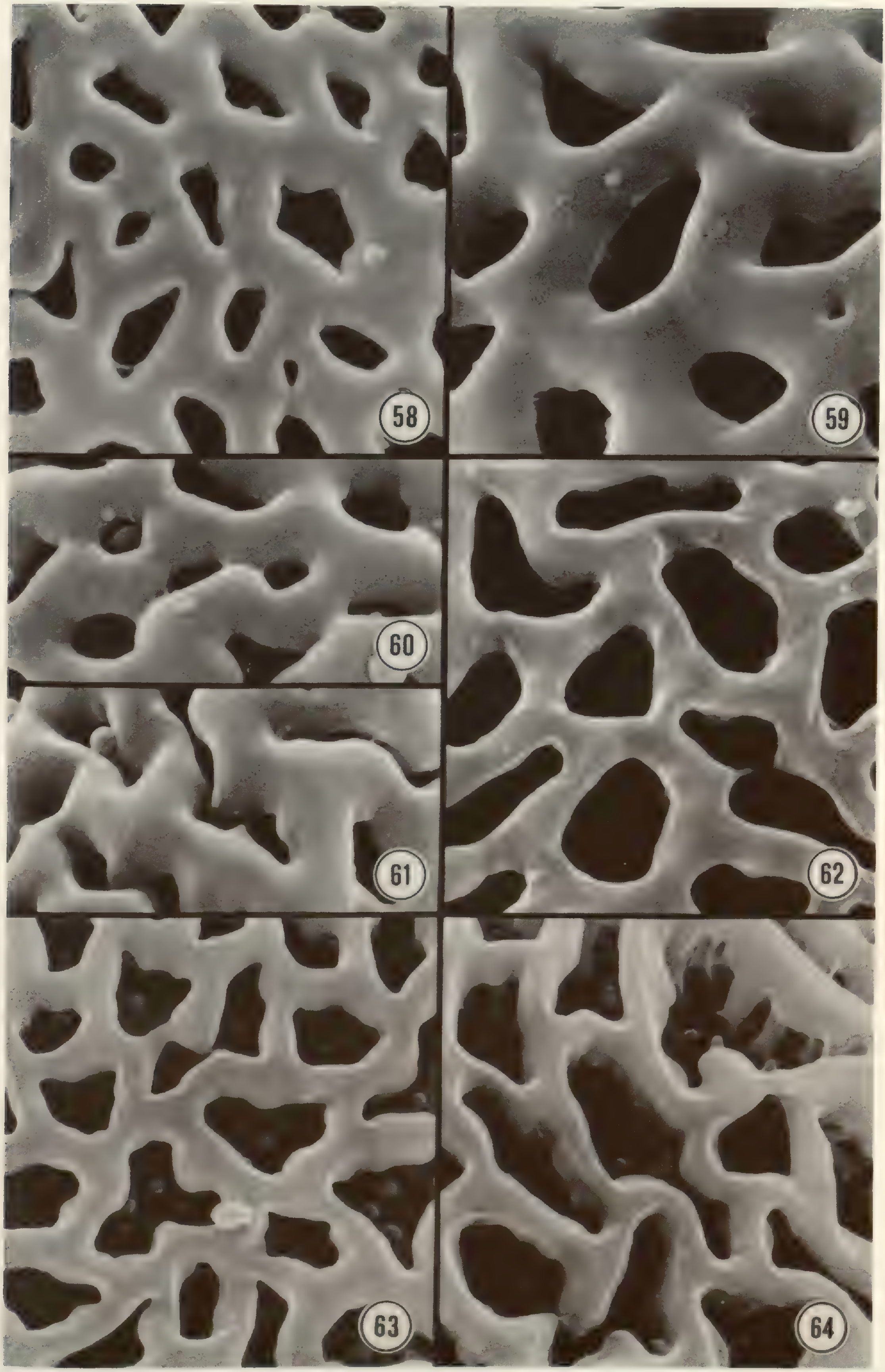
FIGURES 58–64. Exine surface of Type III pollen of *Virola* Aubl.—58. *V. sessilis* (A. DC.) Warburg (*Malme 2007b*, P-2730); ×16,000.—59. *V. subsessilis* (Benth.) Warburg (*Prance & Silva 58503*, P-2732); ×16,000.—60. *V. melinonii* (Benoist) A. C. Smith (*Pires et al. 50526*, P-2725); ×12,000.—61. *V. officinalis* Warburg (*Martius 183*, P-2831); ×12,000.—62. *V. oleifera* (Schott) A. C. Smith (*Glaziou 12140*, P-2000); ×12,000.—63. *V. multiflora* (Standl.) A. C. Smith (*Schipp 279*, P-1986), note free-standing columellae; ×8,000.—64. *V. venosa* (Benth.) Warburg, (*Pires et al. 50550*, P-2005), note free-standing columellae; ×8,000.

FIGURES 65–72. SEM nonapertural exine sections of *Virola* Aubl.—65. *V. mollissima* (A. DC.) Warburg (*Klug 3128*, P-2727).—66. *V. elongata* (Benth.) Warburg (*Prance et al. 14081*, P-2010), note rounded end of columella to left and granular inner surface of tectum.—67, 72. *V. peruviana* (A. DC.) Warburg (*Schultes 6031*, P-2013), 67, note granular inner surface of tectum, 72, tangential section through interstitium looking at inner surface of tectum.—68. *V. oleifera* (Schott) A. C. Smith (*Glaziou 12140*, P-2000).—69. *V. glaziovii* Warburg (*Maguire et al. 56267*, P-2003), note inner surface of nexine at bottom and columella pendulous from inner surface of tectum in the center.—70. *V. koschnyi* Warburg (*Peck 373*, P-1985), partial tangential section through middle of interstitium.—71. *V. divergens* Ducke (*Krukoff 1120*, P-1987), note circular depressions left in surface of nexine by separation of weakly attached columellae. All ×16,000 except Fig. 69, which is ×24,000.

FIGURES 73–77. TEM exine sections of *Virola divergens* Ducke (*Krukoff 1120*, P-1987).—73. Whole grain exine section, showing aperture at top, ×5,000.—74, 76. Nonapertural exine sections, showing very thin, partially finely lamellate nexine, moderately thick columellate interstitium, and average to moderately thick tectum; note conspicuous, small, spherical, intra-exinous cavities in sexine; 74, ×16,000, 76, ×18,000.—75. Apertural exine section, showing extremely thin nexine and reduced and much disorganized sexine, ×19,000.—77. Nonapertural exine, tangential section through tectum, showing spherical, intra-exinous, sexinous cavities, ×16,000.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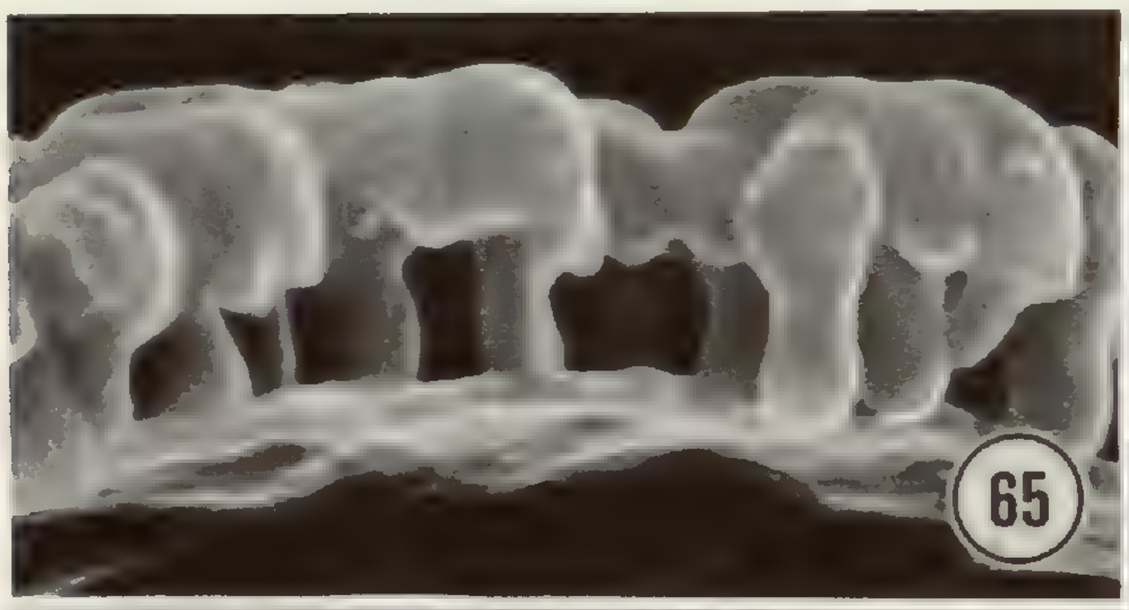
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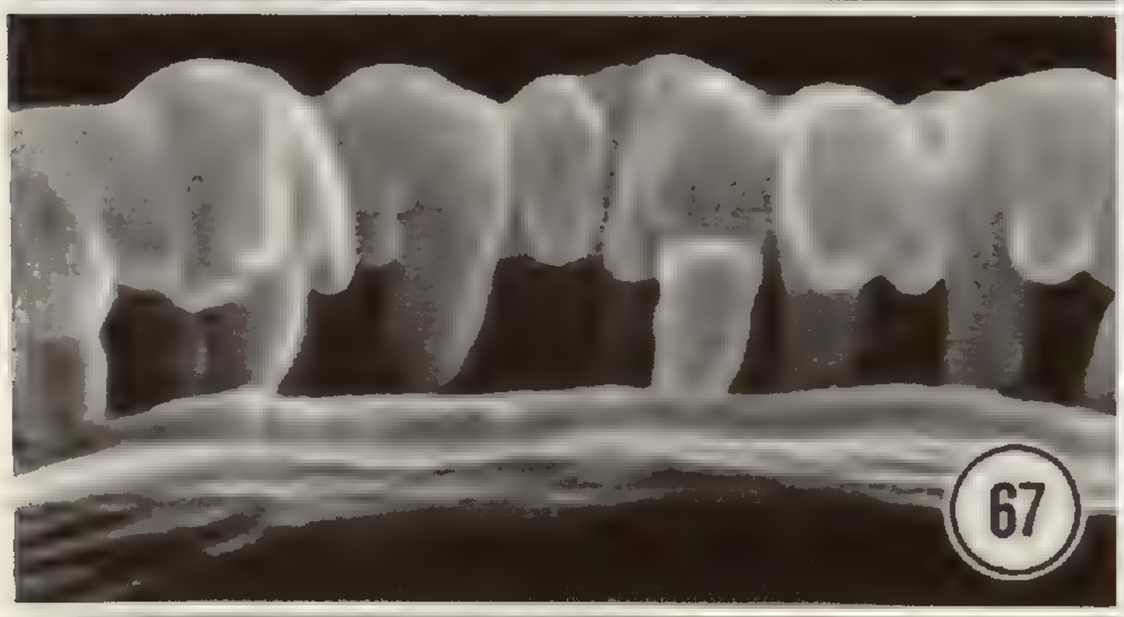
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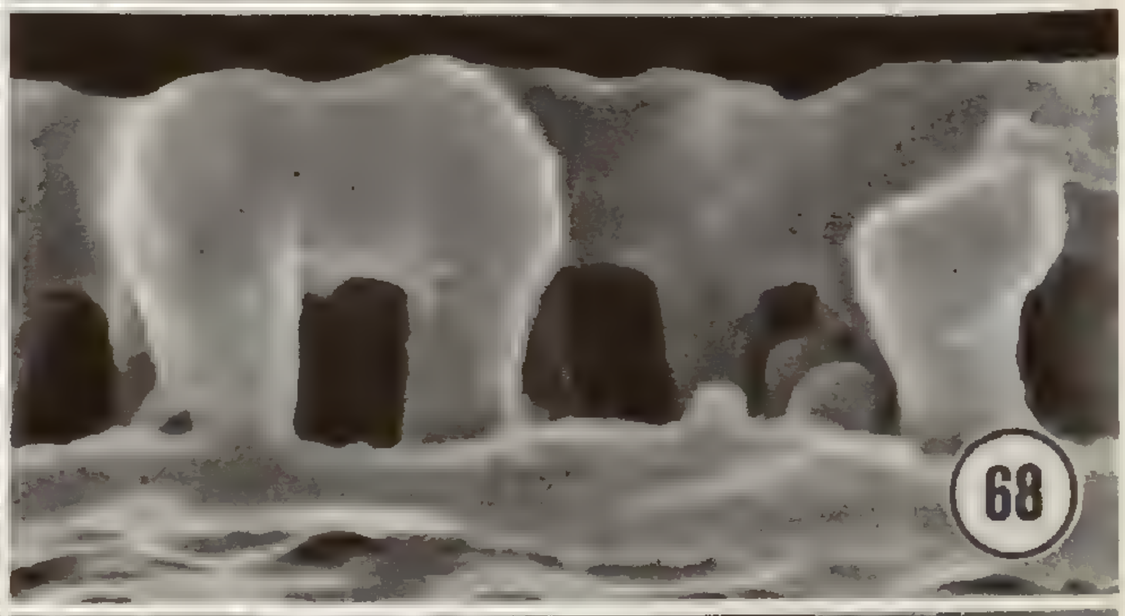
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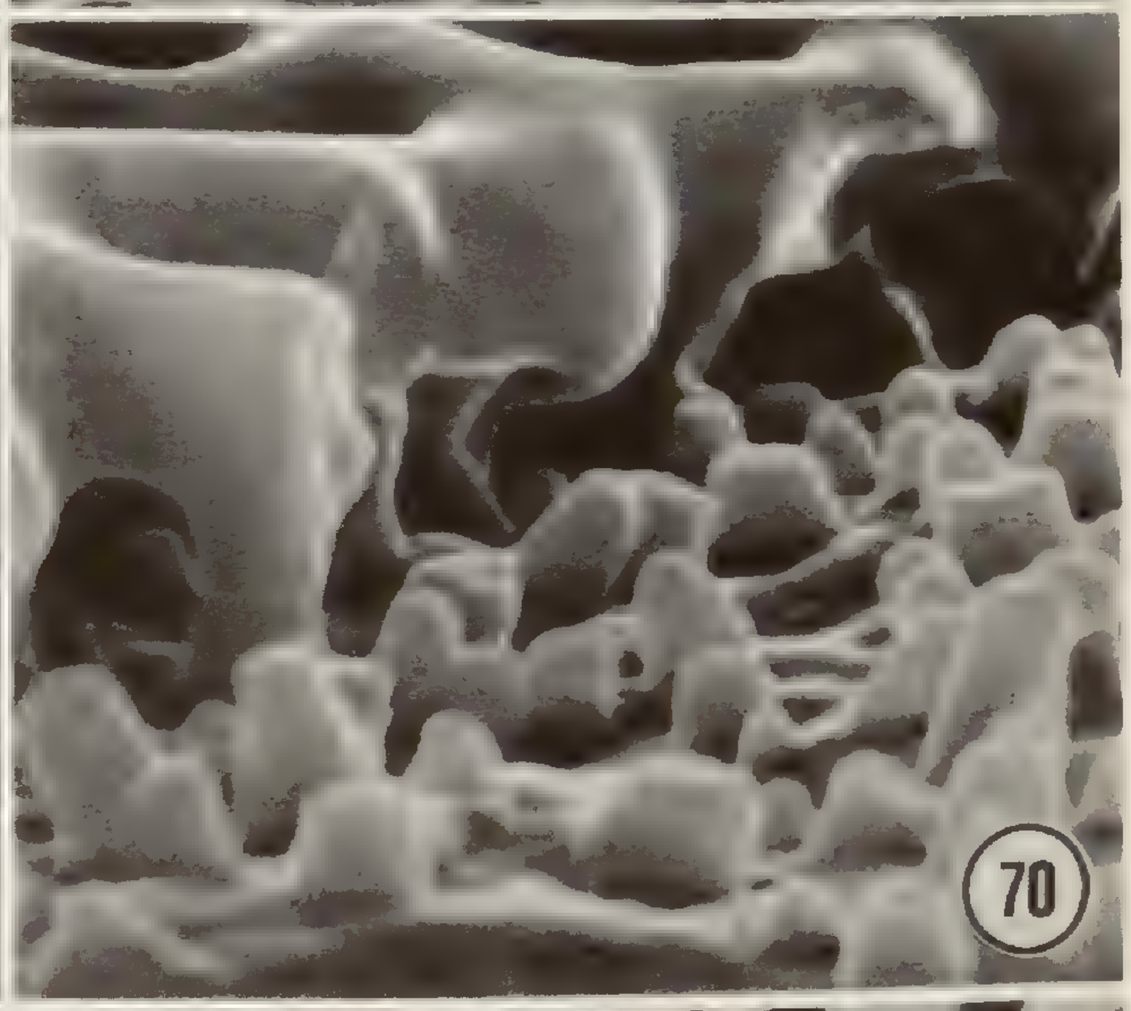
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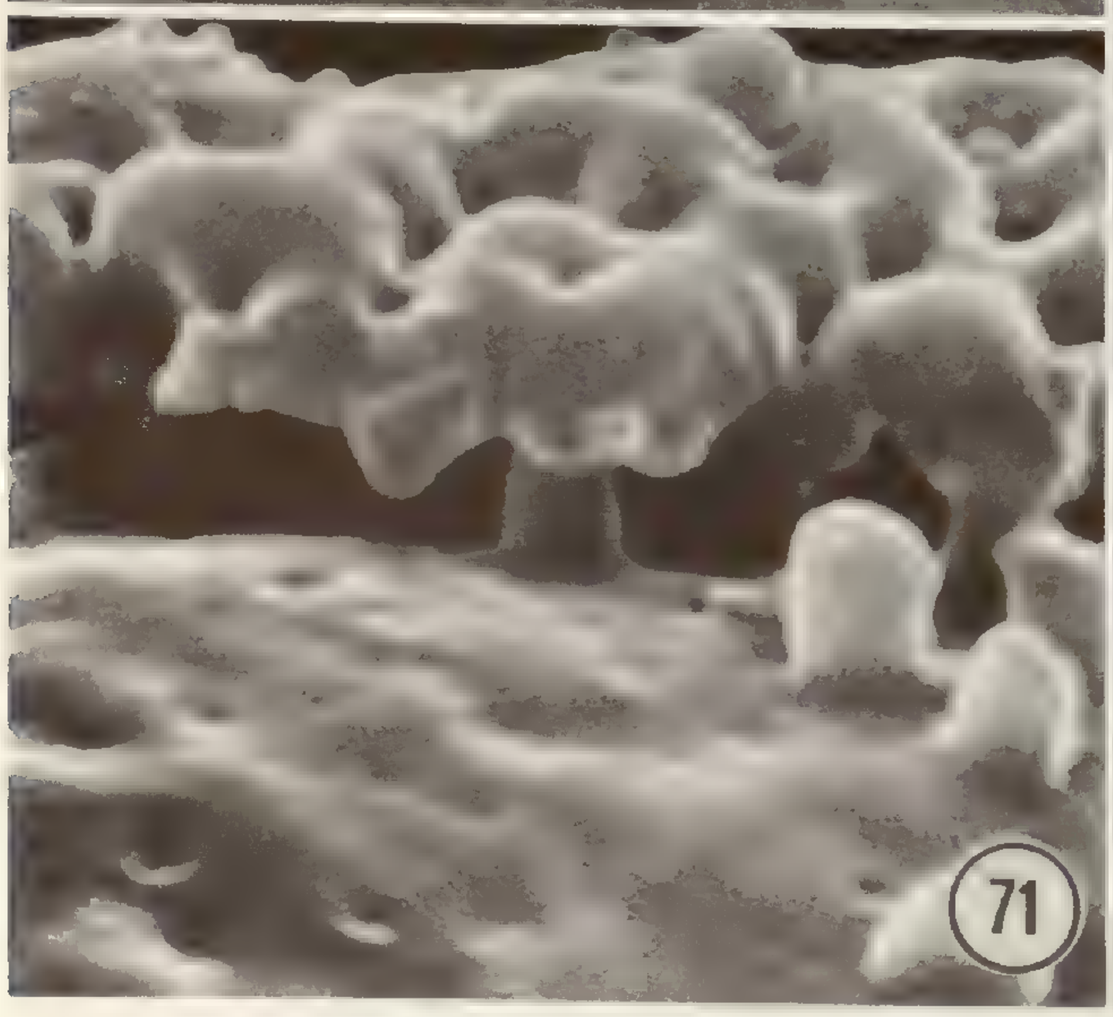
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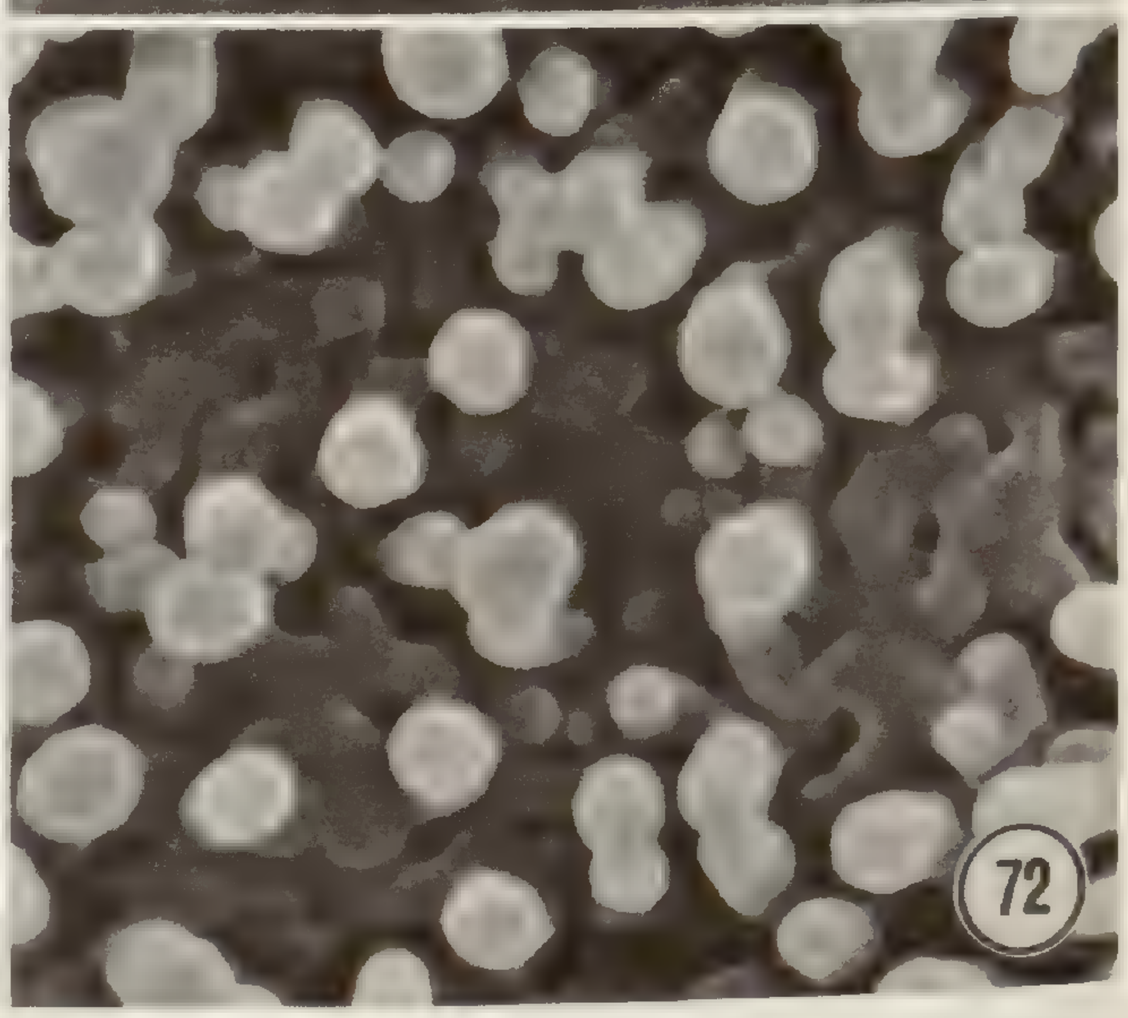
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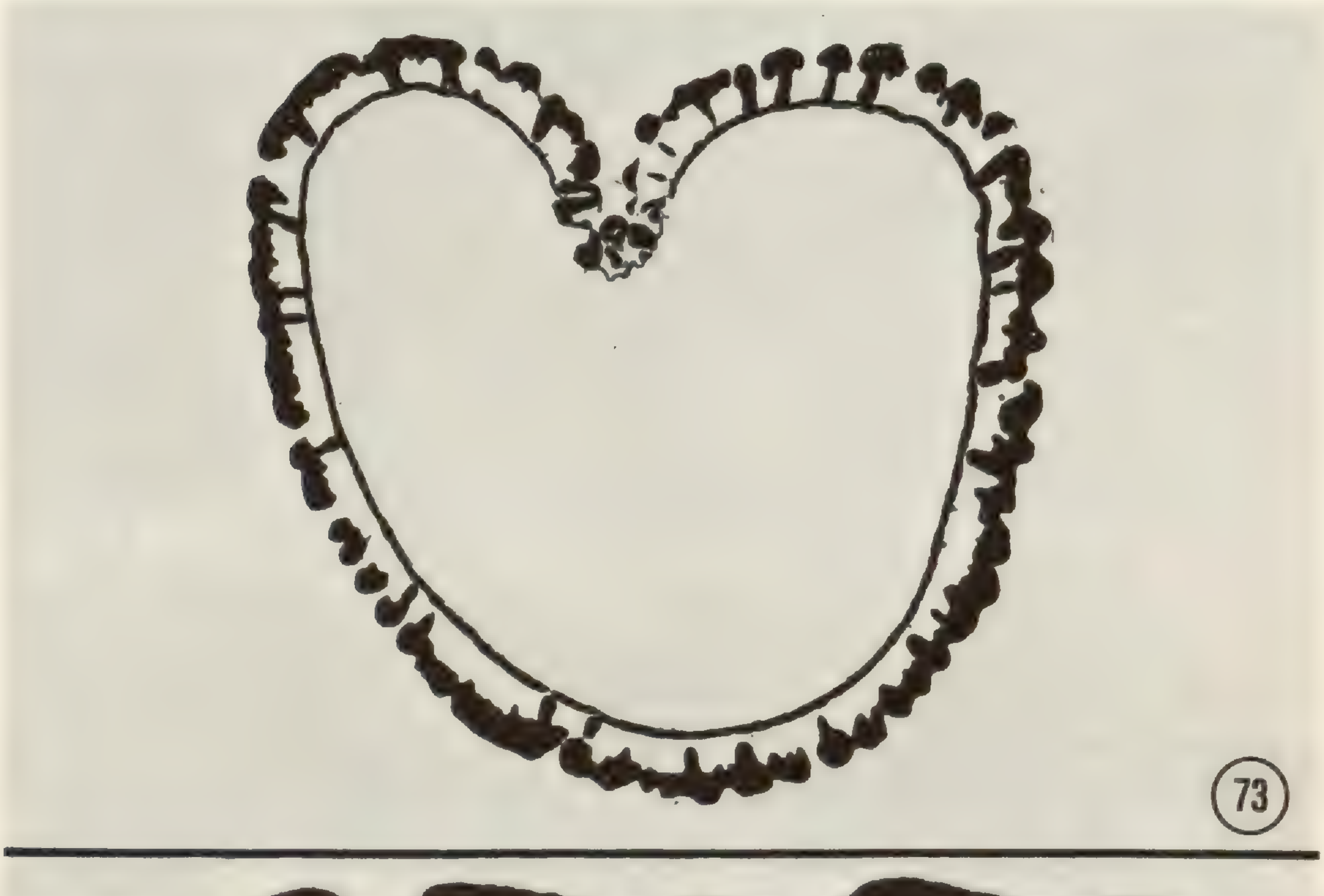
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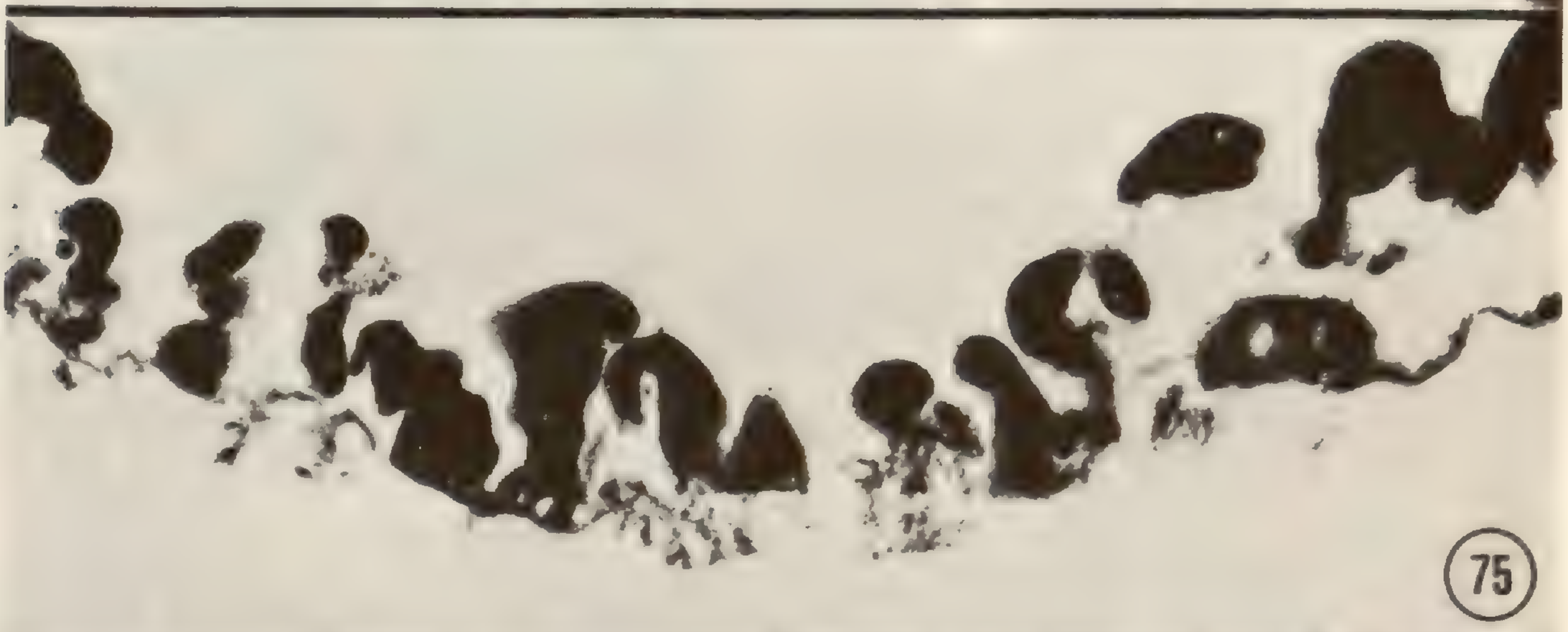
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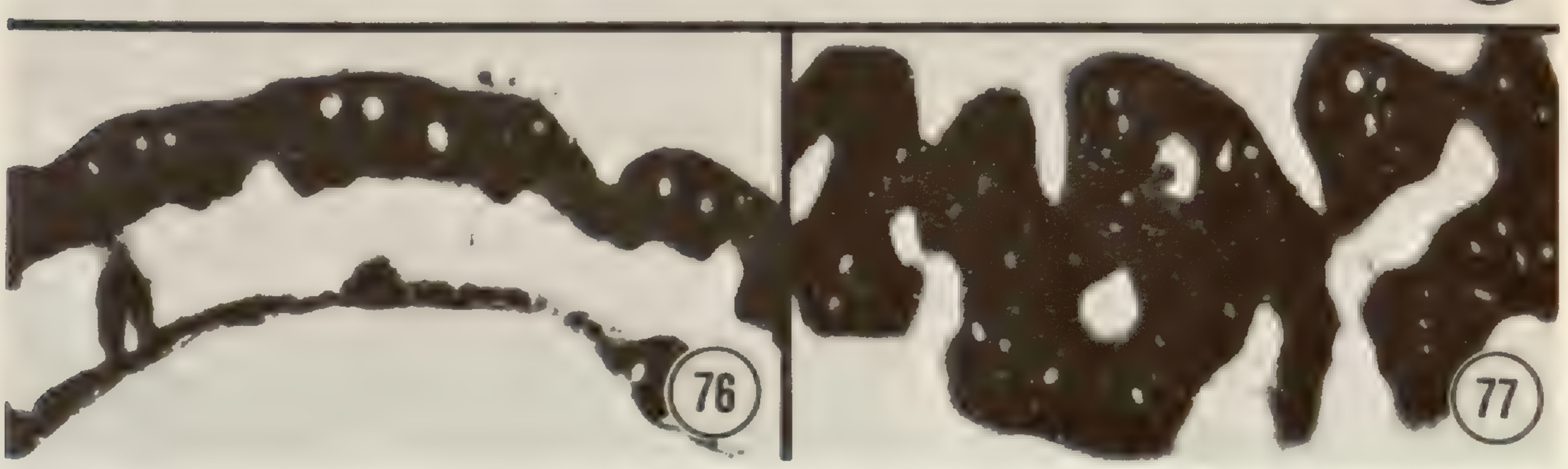
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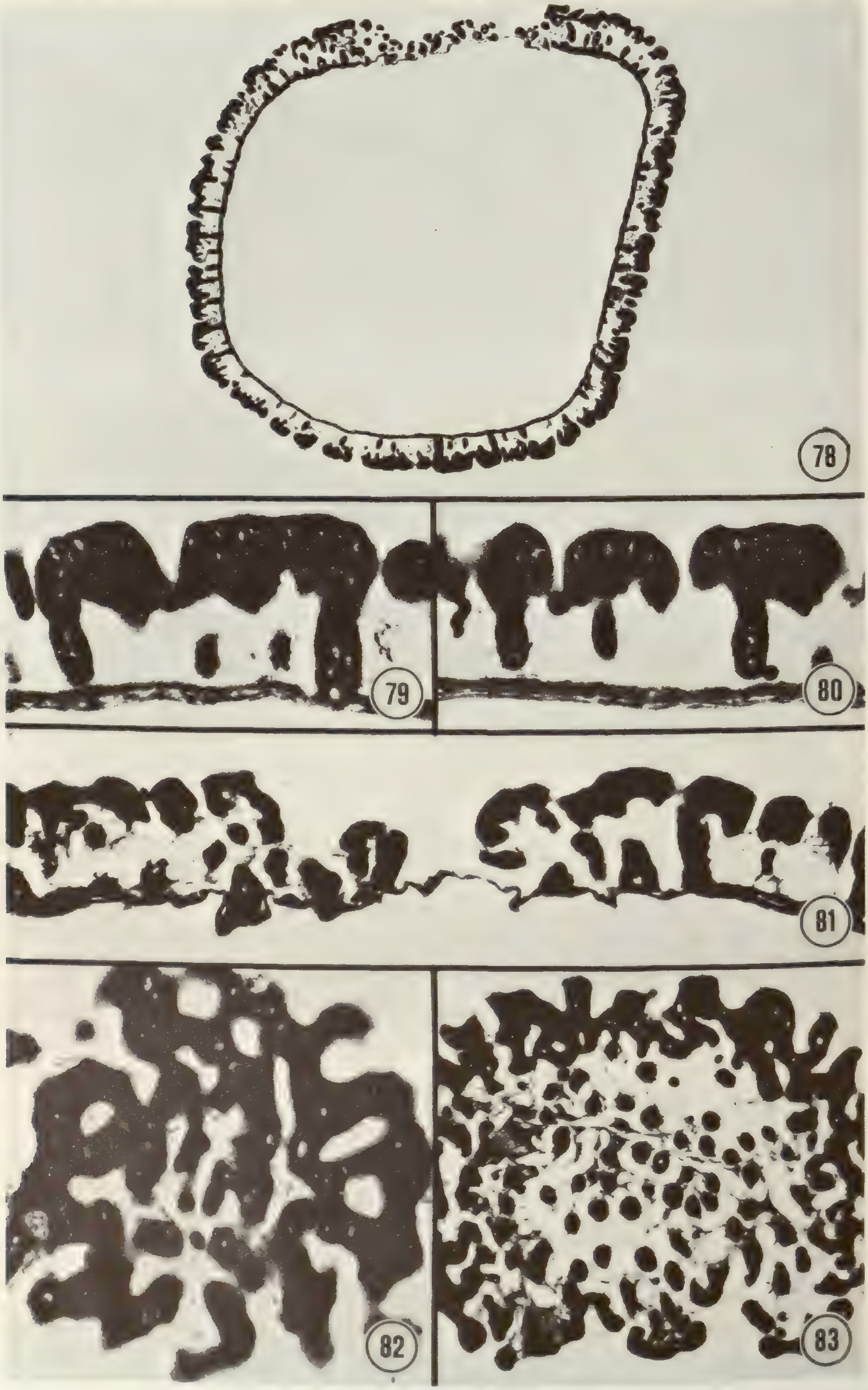
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TABLE 1. Arrangement of *Virola* species according to pollen type.[a]

Pollen Type I	
V. calophylla (3)	*V. loretensis* (1)
V. cuspidata (2)	*V. macrocarpa* (3)
V. divergens (1)	*V. mollissima* (1)
V. duckei (4)	*v. peruviana* (2)
V. elongata (2)	*V. sebifera* (2)
Pollen Type II	
V. calophylloidea (3)	*V. minutiflora* (4)
V. carinata (5)	*V. multinervia* (4)
V. flexuosa (4)	*V. pavonis* (5)
V. glaziovii (5)	*V. surinamensis* (5)
V. malmei (5)	*V. weberbaueri* (2)
Pollen Type III	
V. guatemalensis (5)	*V. officinalis* (4)
V. koschnyi (4)	*V. oleifera* (5)
V. melinonii (5)	*V. sessilis* (6)
V. multiflora (5)	*V. subsessilis* (6)
V. nobilis (5)	*V. venosa* (5)

[a] Numbers in parentheses after each species refer to placement in species groups recognized by Smith (1938).

DISCUSSION

Apertures.—Pollen of *Compsoneura* and *Virola* is usually sulcate (Figs. 1, 3–4, 25–28, 31–33, 37–38) with an aperture that is sharply defined externally (Figs. 1, 25–26, 29–30, 39–40), although sometimes, particularly in *Virola*, the pollen may be more or less sulcoidate with the aperture less evident externally.

Shape, Polarity, and Symmetry.—The pollen of the two genera studied is usually boat-shaped (Figs. 3, 37–38) although sometimes it is more or less globose-spherical (Figs. 5, 34–36, 41–42). Sometimes the pollen grains of both of these genera are more or less rectangular (Figs. 25–26, 28) or triangular in outline with a straight apertural face and a markedly convex nonapertural face (Fig. 27). The unusual triangular-rectangular shape of some mature myristicaceous pollen grains may be related to the unusual planar orientation of their sulcate apertures, as suggested by Kuprianova (1967) (cf. also Walker & Walker, in press, 3). Polarity of their pollen is always more or less heteropolar, while symmetry is generally bilateral.

Size.—Pollen grains of both genera are medium-sized to small. *Compsoneura* pollen averages 24 μm and ranges from 21–27 μm, with the largest grains in *C.*

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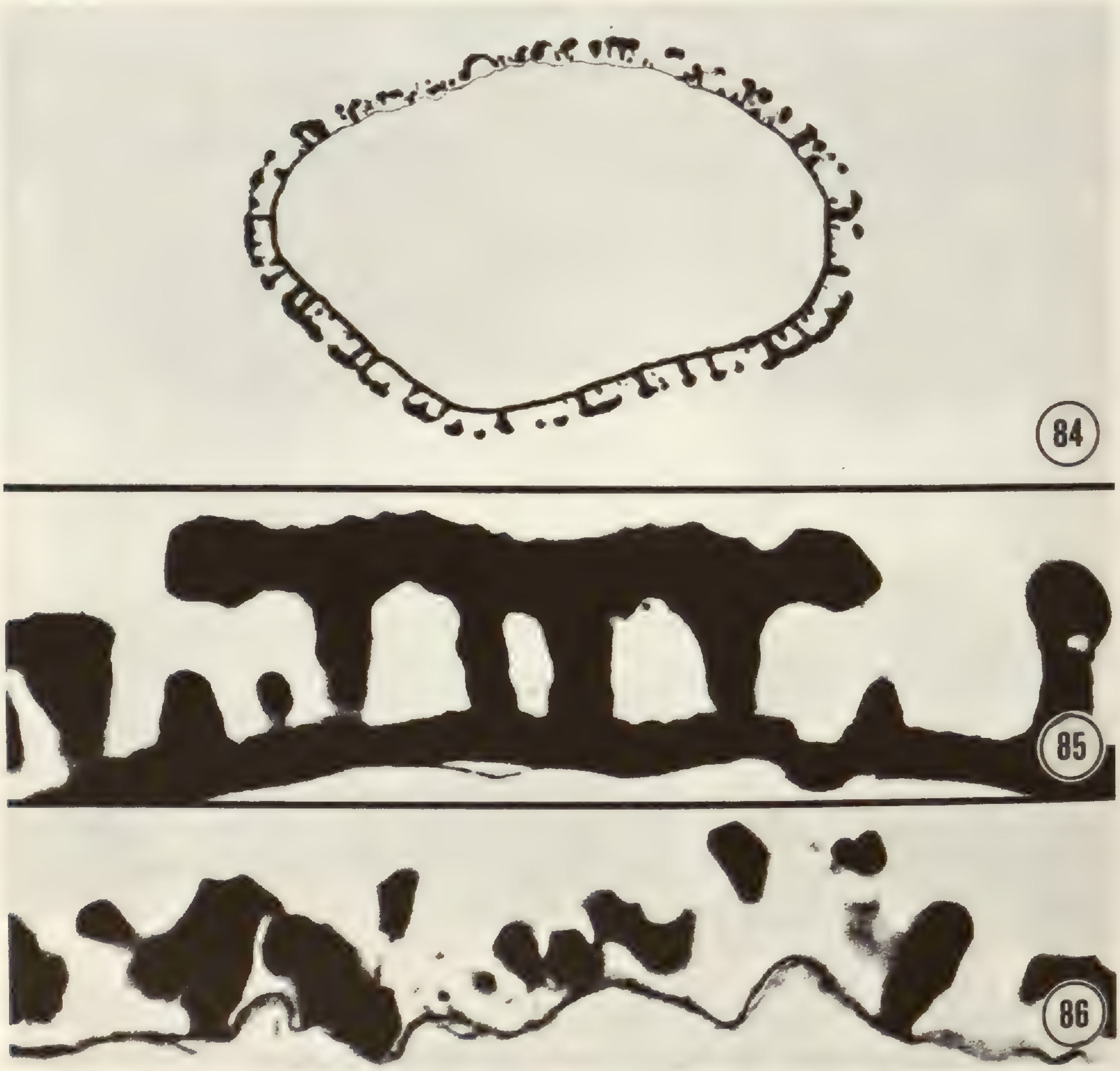
FIGURES 78–83. TEM exine sections of *Virola peruviana* (A. DC.) Warburg (*Schultes 6031*, P-2013).—78. Whole grain exine section, showing aperture at top, ×4,000.—79–80. Nonapertural exine section, showing very thin, finely lamellate nexine, moderately thick interstitium with pendulous columellae, and average to moderately thick tectum; note conspicuous, small, spherical, intra-exinous cavities in sexine, both ×20,000.—81. Apertural exine section, showing extremely thin nexine and reduced and much disorganized sexine, ×14,000.—82–83. Nonapertural exine tangential sections through tectum (82) and interstitium (83), showing spherical, intra-exinous, sexinous cavities; 82, ×19,000, 83, ×13,000.

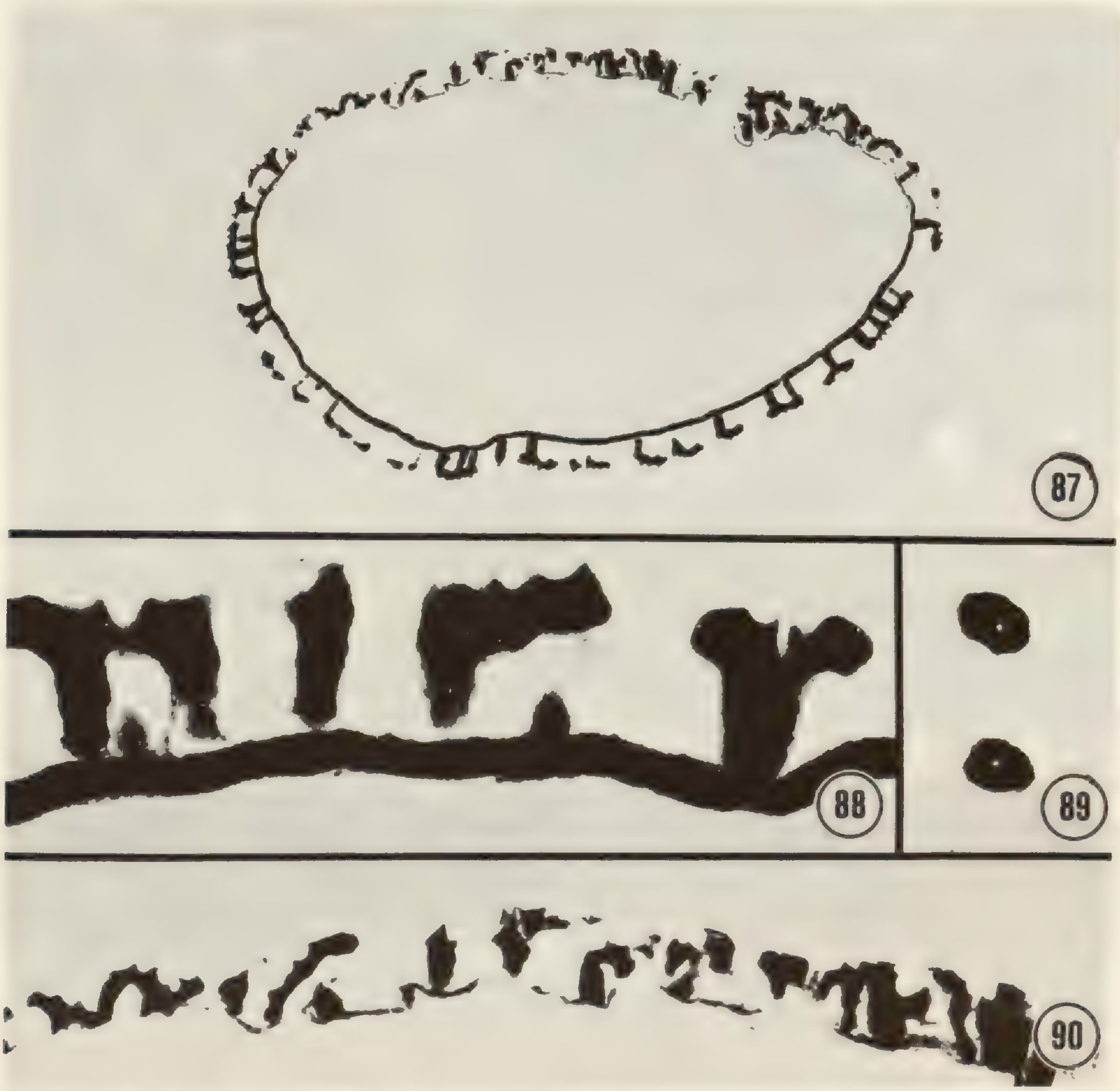


FIGURES 84–86. TEM exine sections of *Virola carinata* (Benth.) Warburg (*Ule 7988*, P-2007).—84. Whole grain exine section, showing aperture at top left, ×3,400.—85. Nonapertural exine section, showing moderately thin, essentially solid nexine, moderately thick columellate interstitium, and average to moderately thick tectum, ×21,000.—86. Apertural exine section, showing extremely thin nexine and reduced and much disorganized sexine, ×20,000.

sprucei and the smallest in *C. mutisii*. *Compsoneura* section *Compsoneura* has slightly larger pollen on the average (with a mean for the section of 25 μm), while the pollen of *Compsoneura* section *Coniostele* is slightly smaller on the average (with a mean for the section of 23 μm). Pollen of *Virola* averages 27 μm and ranges from 22–35 μm, with the largest grains in *V. koschnyi* and *V. guatemalensis* and the smallest grains in *V. calophylloidea*.

Pollen-Unit.—Pollen of both *Compsoneura* and *Virola* is shed as solitary grains or monads (Figs. 1–6, 25–28, 31–38, 41–42).

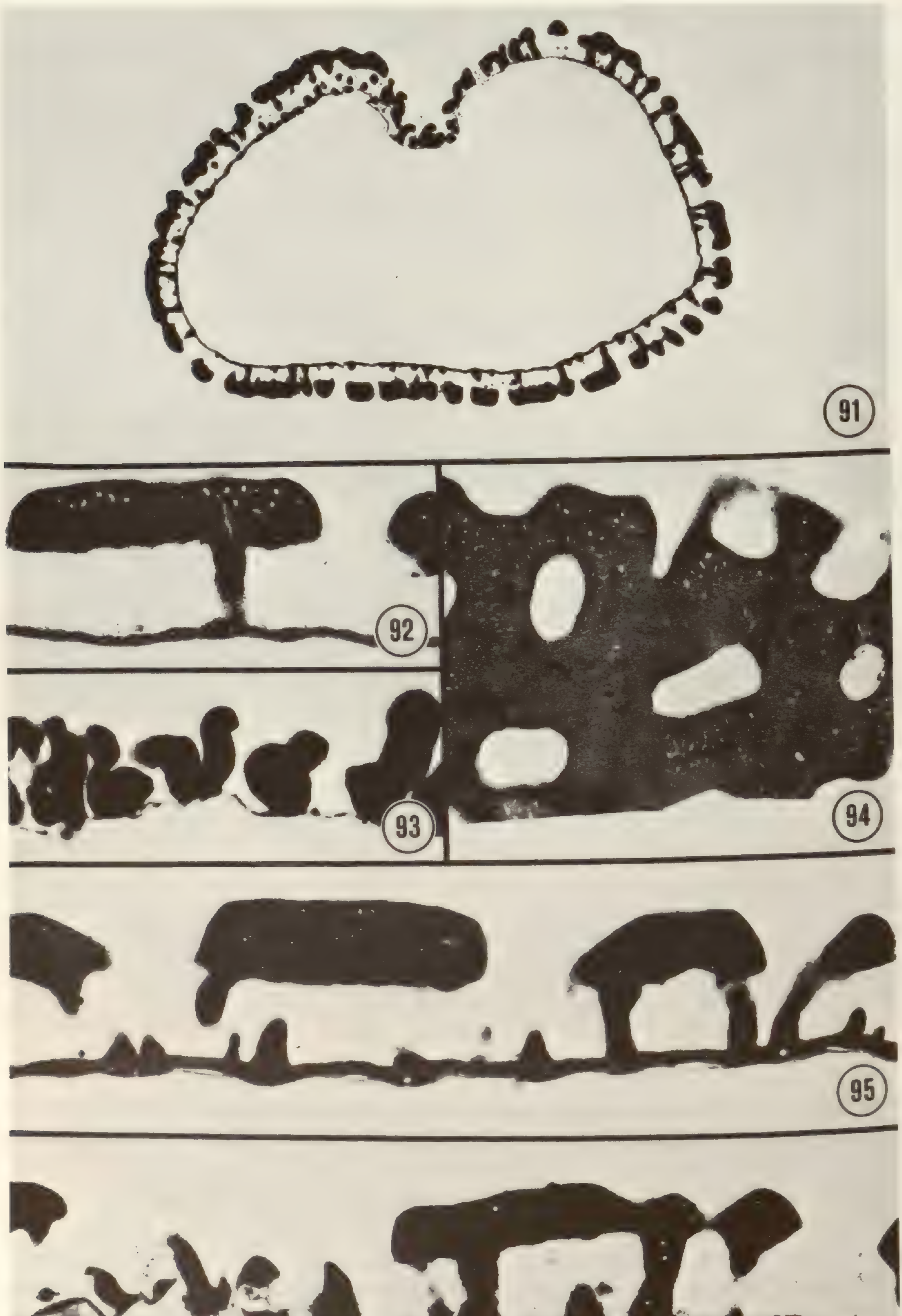
Exine Sculpturing.—In *Compsoneura* the exine is mostly reticuloid (Figs. 7, 10), less commonly definitely reticulate and then sometimes with finely banded muri (Fig. 12). Pollen of *C. excelsa* (Fig. 11) and *C. ulei* (Fig. 12), both of which belong to section *Coniostele* with connate anthers, has decidedly larger tectal



FIGURES 87–90. TEM exine sections of *Virola weberbaueri* Markgraf (*Tessmann 4339*, P-2734).—87. Whole grain exine section, showing aperture at top, ×3,500.—88. Nonapertural exine section, showing moderately thin, solid nexine, moderately thick columellate interstitium, and average to moderately thick tectum, ×20,000.—89. Tangential section through two columellae, showing minute, spherical, intra-exinous cavities, ×19,000.—90. Apertural exine section, showing extremely thin nexine and reduced and much disorganized sexine, ×10,000.

perforations and is more semitectate-reticulate than is the pollen of the species of *Compsoneura* which belong to section *Compsoneura* (Figs. 7–10), which has distinct anthers.

The pollen of *Virola* exhibits a great range of exine sculpturing types and in fact its species may be divided into three different pollen types based upon differences in exine sculpturing patterns (Table 1). Species of Pollen Type I (Figs. 43–49) have basically tectate-perforate pollen grains, although sometimes they may be more or less reticuloid in their sculpturing (Figs. 47, 49). The exine of pollen in this group is usually psilate, although sometimes conspicuous granules may be present on the surface (Fig. 48). Pollen Type II is characterized by pollen which is tectate-perforate to semitectate and which has banded (Figs. 50–52) to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beaded (Figs. 53–54) muri, that occasionally may even have bands which are coarsely granulate (Figs. 55–57). Pollen of the last type, Pollen Type III, is semitectate-reticulate and has psilate muri (Figs. 58–64). Occasionally *Virola* pollen, especially in species with Type III pollen grains, has evident, free-standing columellae that are visible through the lumina of the reticulum, e.g., *V. multiflora* (Fig. 63) and *V. venosa* (Figs. 42, 64).

Exine Structure.—*Compsoneura* (Figs. 13, 20, 23) and *Virola* (Figs. 65, 74, 79–80, 85, 88, 92, 95) have a columellate exine, although frequently the columellae in both genera are only weakly attached to the basal nexine and may even leave circular depressions in its surface upon separation (Figs. 14, 71). Often the columellae in these two genera appear to be pendulous (Figs. 15, 69, 74, 80) from the inner surface of the tectum, which frequently exhibits granules (Figs. 16, 66–67) as well as columellae.

In the nonapertural exine *Compsoneura* generally has an average nexine, an average to moderately thick interstitium, and an average tectum (Figs. 15, 20, 23), while in *Virola* on the average the nexine is generally very thin, the interstitium is moderately thick, and the tectum is average to moderately thick (Figs. 66–67, 74, 79–80, 85, 88, 92, 95). In *Virola* the nexine may be either partially finely lamellate (Figs. 74, 79–80) or essentially solid (Figs. 85, 88), while in *Compsoneura* the nexine is generally essentially solid (Figs. 20, 23).

Small, spherical, intra-exinous cavities are frequently very conspicuous in the pollen of *Virola* (Figs. 74, 76–77, 79–80, 82–83), although sometimes they may be less conspicuous (Figs. 92, 94–96) or almost absent (Figs. 85, 88–89). Although in *Compsoneura* such intra-exinous cavities are also basically present, they are always inconspicuous (Figs. 20, 23).

In both genera the apertural exine has an extremely to very thin nexine and a reduced and much disorganized sexine (Figs. 19, 21–22, 24, 73, 75, 78, 81, 84, 86–87, 90–91, 93, 96).

Exine Stratification.—The exine in both *Compsoneura* and *Virola* is wholly ektexinous and no endexine is present.

Conclusions

Study of the pollen of the American myristicaceous genera *Compsoneura* and *Virola* supports the idea that these two genera are closely related. Palynological features which they have in common include (1) sulcate apertures, (2) usually boat-shaped and frequently more or less triangular, heteropolar, bilateral pollen grains, (3) medium-sized to small pollen, (4) reticuloid to reticulate exine sculp-

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Figures 91–96. TEM exine sections of *Virola* Aubl.—91–94. *V. sessilis* (A. DC.) Warburg (*Malme 2007b*, P-2730).—95–96. *V. koschnyi* Warburg (*Peck 373*, P-1985).—91. Whole grain exine section, showing aperture at top, ×3,300.—92, 95. Nonapertural exine sections, showing very thin, essentially solid nexine, moderately thick columellate interstitium, and average to moderately thick tectum; note minute, spherical, intra-exinous cavities; 92, ×19,000, 95, ×13,000.—93, 96. Apertural exine sections, showing extremely thin nexine and reduced and much disorganized sexine, note fine nexinous lamellae to the right in Fig. 96; 93, ×16,000, 96, ×15,000.—94. Nonapertural exine tangential section through tectum, showing minute, spherical, intra-exinous cavities, ×15,000.

turing that sometimes consists of banded or even beaded muri, (5) columellate exine structure with columellae that are weakly attached to the nexine, (6) tectate-perforate to semitectate pollen grains, and (7) apertural exine with an extremely to very thin nexine and a reduced and disorganized sexine that results in an aperture which is sharply delimited externally.

Within *Compsoneura*, pollen of the florally more advanced section *Coniostele* (Figs. 5–6, 11–12) is decidedly more advanced than that of the florally more primitive *Compsoneura* section *Compsoneura* (Figs. 1–4, 7–10).

Virola has a wide range of exine sculpturing patterns (Figs. 43–64), which allow recognition of three groups of species within the genus based on pollen morphology. To a certain extent these pollen groups show some degree of correlation with the species groups proposed by Smith (1938) (cf. Table 1). For example, all species of *Virola* with Type I pollen fall in Smith's Species Groups 1, 2, or 3 except for *V. duckei*, which has Type I pollen but is a member of Smith's Species Group 4. Only two examined species in Smith's Species Groups 1, 2, and 3 did not possess pollen of Type I, and these two species (*V. calophylloidea* and *V. weberbaueri*) both have pollen of Type II. Interestingly Smith (1938) stated that the shape of the staminate perianth of *V. weberbaueri* was not typical of his Species Group 2 and he therefore also keyed this species in his Species Group 5, which not only has pollen exclusively of Type II or III but which also contains *V. pavonis*, which has pollen with the same kind of distinctive granulate-banded muri as occur in *V. weberbaueri* (cf. Figs. 55–57). Except for *V. duckei* as mentioned above, all examined members of Smith's Species Groups 4, 5, and 6 have pollen of Type II or III.

Within the *Virola* species which have Type II pollen grains, pollen of *V. glaziovii* (Fig. 50), *V. malmei* (Fig. 51), and *V. carinata* (Fig. 52) is only very faintly banded, while pollen of *V. surinamensis*, *V. minutiflora*, *V. flexuosa*, and *V. multinervia* (Fig. 53) is more pronouncedly banded. The banded muri of the pollen of *V. calophylloidea* (Fig. 54) is more or less distinctive, while the coarsely granulate-banded muri of the pollen of *V. weberbaueri* (Figs. 55, 57) and *V. pavonis* (Fig. 56) sets these two species apart. Within the species with Type III pollen, *V. sessilis* (Fig. 58) and *V. subsessilis* (Fig. 59) have a slightly different type of exine sculpturing pattern that seems to set these two species somewhat apart from the other species with Type III pollen grains.

Interestingly, the small, spherical, intra-exinous cavities that are generally present in the sexine of *Virola* pollen grains are very conspicuous in the pollen of *V. divergens* (Figs. 74, 76–77) and *V. peruviana* (Figs. 79–80, 82–83), both of which belong to Pollen Type I, while these cavities are less conspicuous in the pollen of *V. sessilis* (Figs. 92, 94) and *V. koschnyi* (Figs. 95–96), which belong to Pollen Type III, and they are inconspicuous in the pollen of *V. carinata* (Fig. 85) and *V. weberbaueri* (Figs. 88–89), which belong to Pollen Type II. Also the nonapertural nexine in *V. divergens* (Fig. 74) and *V. peruviana* (Figs. 79–80) with Type I pollen is more conspicuously lamellate and thinner than the nonapertural nexine in *V. carinata* (Fig. 85) and *V. weberbaueri* (Fig. 88), which both have Type II pollen grains, while the nonapertural nexine of both *V. sessilis* (Fig. 92) and *V. koschnyi* (Fig. 95), which belong to Pollen Type III, is as thin as the nexine in *V. divergens* and *V. peruviana* but not as pronouncedly lamellate.

Although the pollen of the palynologically most primitive species of *Compsoneura* and *Virola* is externally more or less indistinguishable (cf. Figs. 1–2 and 7 of *Compsoneura capitellata* with Figs. 25 and 43 of *Virola calophylla*), pollen of *Compsoneura* can be separated from that of *Virola* on the basis of the following characters: (1) the thickness of the nonapertural nexine in *Compsoneura* pollen is average, with the nexine constituting about a third of the total exine thickness (Figs. 20, 23), while the nonapertural nexine in *Virola* (Figs. 74, 79–80, 85, 88, 92, 95) is generally very thin and usually makes up less than 15% of the total thickness of the nonapertural exine, (2) the nexine may be more or less conspicuously lamellate (Figs. 74, 79–80, 96) or not (Figs. 85, 88, 92) in *Virola* (although nexinous lamellae are significantly most conspicuous in the species of *Virola* which are sculpturally most similar to *Compsoneura* such as *V. divergens* and *V. peruviana*), while nexinous lamellae are always more or less inconspicuous in *Compsoneura* (Figs. 20, 23), and (3) spherical, intra-exinous, sexinous cavities are generally conspicuous in *Virola* (Figs. 74, 76–77, 79–80, 82–83, 92, 94, 95–96), especially in the species which are sculpturally most similar to *Compsoneura*, while such cavities are very inconspicuous in *Compsoneura* (Figs. 20, 23). The markedly semitectate-reticulate pollen of the palynologically more advanced species of *Virola* (Figs. 50–64) which belong to Pollen Types II and III of course are usually readily distinguishable from the pollen of *Compsoneura* section *Compsoneura* (Figs. 7–10), although pollen of *Compsoneura* section *Coniostele* (Figs. 11–12) might be confused (at least externally) with the pollen of some species of *Virola* which possess Type II pollen grains (cf. Fig. 12 of *Compsoneura ulei* pollen with Figs. 51 and 53 of *Virola malmei* and *V. multinervia* pollen).

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TAXONOMIC IMPLICATIONS OF BIGNONIACEAE PALYNOLOGY[1,2]

ALWYN H. GENTRY[3] AND A. SPENCER TOMB[4]

ABSTRACT

The neotropical genera of Bignoniaceae are surveyed palynologically and applications of palynology to the taxonomy of the family are reviewed. The family is markedly eurypalynous and pollen morphology is extremely useful taxonomically in generic delimitation. However, most of the divergent pollen types found in the family appear to have evolved independently in different lineages, limiting the applicability of palynological data to tribal and familial classification. The importance of interpreting palynological data in taxonomic context is emphasized. Several generic realignments and informal subtribal groups are proposed based largely on palynological evidence.

Genera of Bignoniaceae are notoriously difficult to recognize (Lawrence, 1951; Gentry, 1973). This has largely been due to taxonomic over-splitting. In fact, there are fewer species per genus in Bignoniaceae than in any other large or medium-sized plant family (Gentry, 1973) and Willis's *Dictionary* (Airy Shaw, 1966) lists 54 monotypic genera. Critical redefinition of genera is clearly the major taxonomic problem in the family. The careful use of pollen morphology has been a valuable tool in generic delimitation and in understanding relationships in the family.

The Bignoniaceae are conspicuously eurypalynous (Buurman, 1977; Tomb & Gentry, in prep.), despite Rendle's (1925) statement to the contrary. Figures 1–9 demonstrate some of the pollen diversity of the family. The taxonomic potential of pollen morphology in Bignoniaceae has long been appreciated, and Urban's (1916) early palynological study of Bignoniaceae is a classic. Pichon (1945), Gomes (1955) and other subsequent workers followed Urban's lead in proposing numerous new genera based on palynological differences. Unfortunately, the lack of any overall understanding of the family has led to repeated taxonomic misinterpretations.

Previous studies of the pollen of this family have relied mostly on light microscopy and some of the misinterpretations of pollen morphology are due to the difficulties of light microscopic analysis. Even though several recent papers on bignon pollen have been based largely on SEM work and have provided taxonomically important new information (Ferguson & Santisuk, 1973; Buurman, 1977), no attempt has yet been made to apply electron microscopic data to the taxonomy of more than a limited representation of the family. Moreover, even some recent workers with Bignoniaceae pollen have misinterpreted taxonomic and palynologic relationships in the family. Thus Mitra (1968) concluded that the family must be polyphyletic on account of its great palynological diversity and the presence of both putatively primitive and advanced pollen types. Suryakanta (1973) emphasized the essential palynological cohesiveness of the family but sug-

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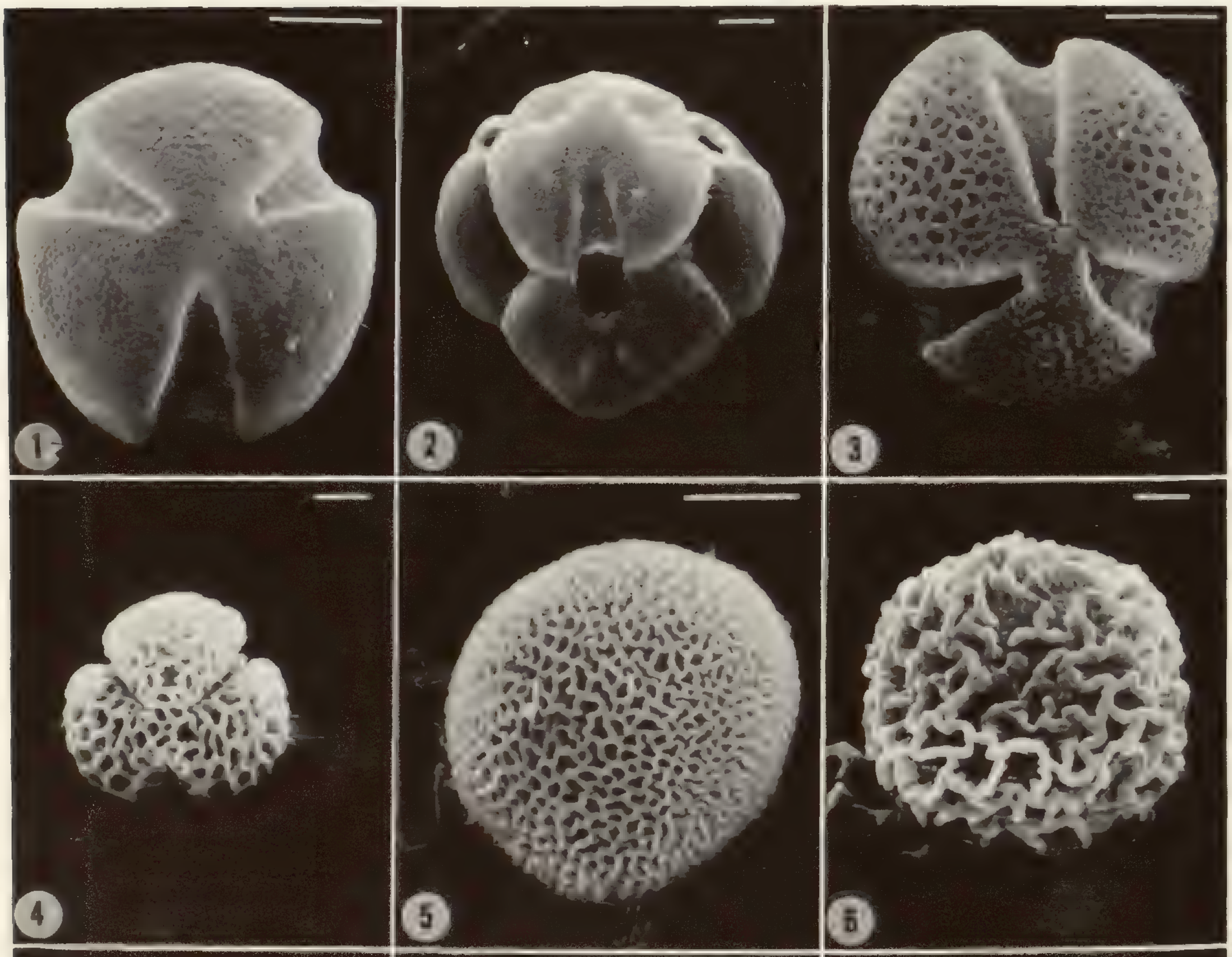
gested an unlikely derivation of Bignoniaceae pollen types from a spiroaperturate ancestral form. Most of these recent studies, even Buurman's (1977) excellent contribution, have been marred by taxonomic errors when dealing with the difficult neotropical taxa.

One major problem which has plagued the interpretation of Bignoniaceae is a conspicuous lack of taxonomic perspective on the part of students of its palynology. Thus, when a palynologist discovered a palynologically atypical species in one genus, it was frequently segregated as a new genus; however, most such species had been erroneously assigned in the first place and could have been reassigned to some other established genus with which they agree both palynologically and morphologically. Such segregate genera as *Blepharitheca* (from *Saldanhaea* but better assigned to *Cuspidaria*, Gentry, 1973), *Nestoria* (from *Memora* but better assigned to *Pleonotoma* (Gentry, 1976c), and *Orthotheca* (see the following paper), provide clear examples.

Another important point made obvious by the present study is that pollen can vary intragenerically as does morphology. Pollen should not be accorded the disproportionate emphasis in generic delimitation which has characterized previous palynological work in the family (Pichon, 1945; Mitra, 1968). On the other hand, palynological variation cannot be ignored, as has been the inclination of traditional taxonomists (Bureau & Schumann 1896–1897; Standley & Williams, 1974). Palynological characters must be evaluated in taxonomic context as one of many potentially significant indicators of evolutionary and systematic relationships.

Crescentia provides a good example of the taxonomic pitfalls of palynological over-reliance. There are two Central American species—*C. alata* with mostly 3-foliolate leaves, and *C. cujete* with simple leaves. These species are so closely related that occasional simple-leaved variants of *C. alata* cannot be separated with certainty from *C. cujete*. The two apparently hybridize in nature and a challenge to the validity of their *specific* segregation would be on stronger grounds than an attempt to separate them generically. However, several palynologically oriented authors have contrasted the 3-colpate pollen of *C. alata* with the (supposedly) inaperturate (Urban, 1916) or multiporate (Mitra, 1968) pollen of *C. cujete* and concluded that these two species constitute separate genera. *Crescentia alata* is either called *Pteromiscus* or, worse, placed in distantly related *Parmentiera* with which it has almost nothing in common except shared tribal and familial characteristics and the 3-colpate pollen. The SEM emphasizes the palynological similarity of *C. cujete* and *C. alata*. The dimensions and exine sculpturing of both species are similar. The main difference is in the number and size of colpi which the SEM reveals to have been misinterpreted. The six colpi of *C. cujete* are each half as long as one of the three colpi of *C. alata* and oriented in the same position. Almost certainly each of the long colpi of *C. alata* has become evolutionarily separated equatorially into two smaller colpi, a relatively minor change clearly unworthy of generic segregation in the absence of any additional evidence.

Anemopaegma provides a similar example. Urban (1916) characterized the genus as inaperturate, based on his light microscopic study. In fact, the type species of the genus, *A. arvense* (examined by Urban under the name *A. mirandum*) proves to have perisyncolpate pollen with the higher resolution of the



FIGURES 1–9. Main pollen types of neotropical Bignoniaceae.—1. *Xylophragma seemannianum*, tricolpate, psilate-foveolate, polar view.—2. *Cuspidaria floribunda*, psilate-foveolate tetrad.—3. *Pyrostegia dichotoma*, tricolpate, finely reticulate, subpolar view.—4. *Martinella obovata*, tricolpate, coarse-reticulate, polar view.—5. *Cydista aequinoctialis*, inaperturate, medium-reticulate.—6. *Distictella magnoliifolia*, inaperturate, coarse-reticulate.—7. *Amphilophium paniculatum*, stephanocolpate, coarse-reticulate, subpolar view.—8. *Amphilophium paniculatum*, stephanocolpate, coarse-reticulate, equatorial view.—9. *Sparattosperma leucanthum*, areolate. Lines in all figures equal 10 μm.

SEM. Most other *Anemopaegma* species are also perisyncolpate, although a few are stephanocolpate. Thus segregation of the colpate species as *Pseudopaegma* is unjustified, even palynologically. These two genera are identical in all other characters and should be merged as has already been suggested (Gentry, 1976c).

An overview of tribal divisions of Bignoniaceae provides the necessary perspective for evaluation of the palynological evidence. The Bignoniaceae are predominantly neotropical (600 out of 800 species) and most of its tribes also are restricted to the New World. The largest tribe, Bignonieae, has 349 species and is entirely neotropical except for one species in the southeastern United States. All genera are exclusively or predominantly tendrillate vines, have anomalous wood anatomy (with radially arranged phloem arms in cross-section), and have fruit dehiscence parallel to the septum. The six species of Old World trees and nontendrillate climbers (*Oroxylum, Hieris, Nyctocalos, Millingtonia*), which are traditionally included here, are probably not closely related to the New World genera and better placed in a separate tribe Oroxyleae (Gentry, 1979b). The second major tribe, Tecomeae, is pantropical in distribution and also includes a few temperate zone genera. Its members are mostly trees and shrubs but also include a few nontendrillate vines which lack anomalous wood anatomy; fruit dehiscence is perpendicular to the septum. Two tribes which are usually lumped together have indehiscent fruits. Crescentieae in the narrow sense (Gentry, 1979b) includes three genera and 33 species of trees and shrubs, mostly in Central America and the West Indies; it is characterized by indehiscent fruits and bat-pollinated flowers. The indehiscent-fruited Madagascar Bignoniaceae (plus *Kigelia* of continental Africa) are independently derived from a different Tecomeae stock and should be treated taxonomically as the tribe Coleeae (Gentry, 1976b). Three neotropical genera (*Schlegelia, Gibsoniothamnus*, and *Synapsis*) of simple-leaved lianas and shrubs, which are usually hemiepiphytic and have berrylike indehiscent fruits, have traditionally been included in Crescentieae. They merit tribal recognition as Schlegelieae and may be closer to the Scrophulariaceae. Finally, two small neotropical genera are usually recognized as monogeneric tribes—Eccremocarpeae with six species in the Andes and Tourrettieae with one species in the Andes and upland Central America. *Eccremocarpus* is a wiry vine with multifoliolate, usually tripinnatisect tendrillate leaves, tubular hummingbird-pollinated flowers, a 1-celled ovary with parietal placentation and a thin-walled ovoid capsule without a septum. *Tourrettia* is an annual herbaceous vine with tendrillate leaves, a 4-loculed ovary, and spiny burlike incompletely dehiscent epizooic fruit. On the basis of morphology, these eight tribes are clearly natural.

The following paragraphs and Table 1 summarize Bignoniaceae palynological types by tribe and genus with different taxonomic assemblages which share a given pollen type indicated. Descriptions of Bignoniaceae pollen types and palynological interpretations have been emphasized in Tomb & Gentry (in prep.) and Buurman (1977). This paper focuses on the systematic utility of Bignoniaceae pollen. The major purpose of this paper is to demonstrate the utility of palynological data in generic and subtribal realignment of the neotropical Bignoniaceae. The following paper in this issue (Gentry, 1979c) formally makes some of these realignments. Species examined for this study are listed in the Appendix.

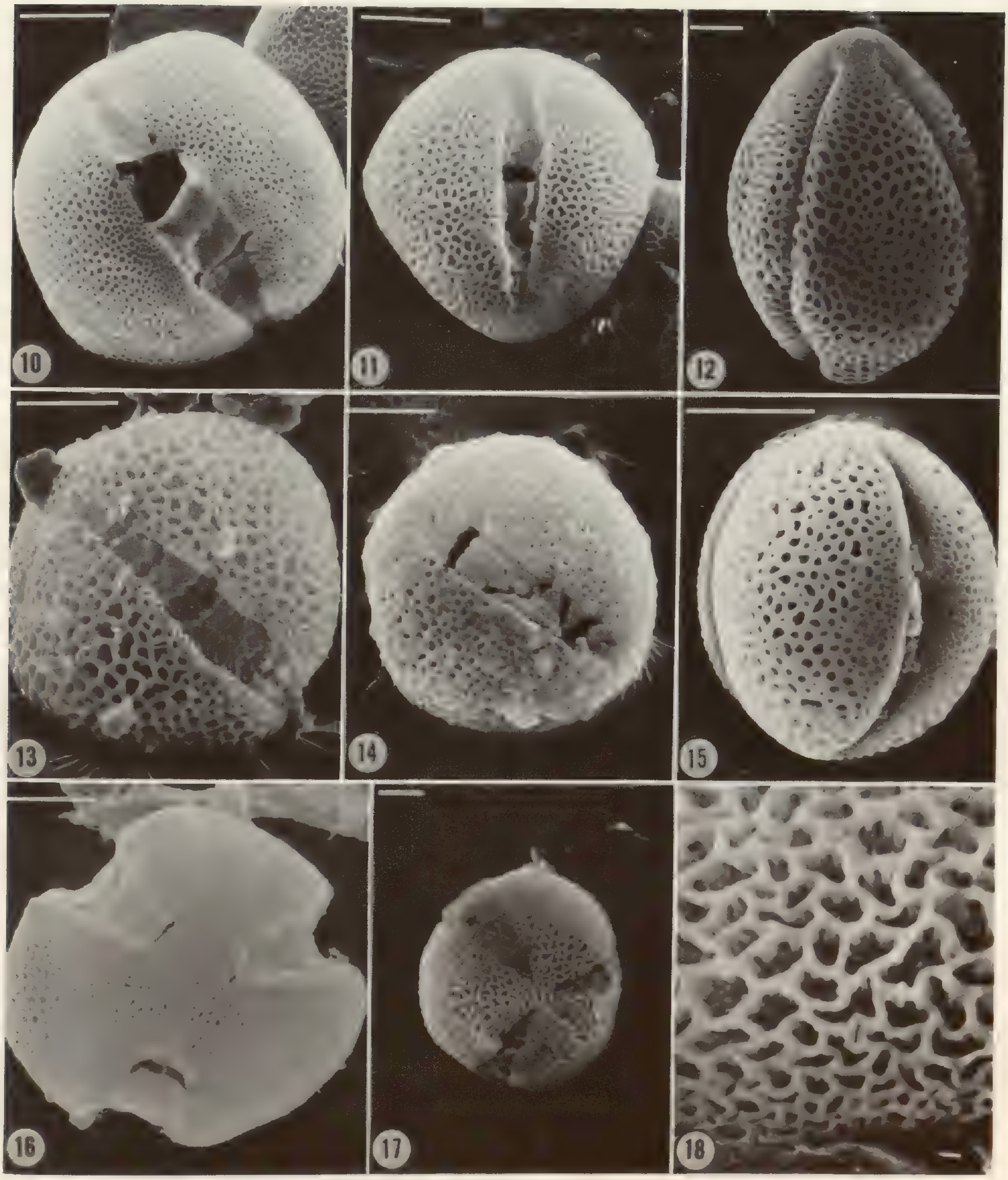
Tecomeae

Genera of the less-specialized tribe Tecomeae are relatively well defined, both morphologically and palynologically. There are only three fundamental pollen

TABLE 1. New World Bignoniaceae pollen types.

Pollen Type	Genera
Psilate and microperforate, 3-colpate (4–6-colpate in *Leucocalanthe*)	BIGNONIEAE: *Arrabidaea, Ceratophytum, Dolichandra, Fridericia, Leucocalanthe, Macfadyena, Manaosella, Melloa, Parabignonia, Paragonia, Paradolichandra, Periarrabidaea, Pseudocatalpa, Setilobus, Spathicalyx, Xylophragma* TECOMEAE: *Digomphia, Jacaranda* ECCREMOCARPEAE: *Eccremocarpus* TOURRETTIEAE: *Tourrettia*
Psilate, 3-colpate tetrads or polyads	*Cuspidaria*
Finely reticulate, 3-colpate (to 4-colpate in *Pyrostegia venusta* and *Roentgenia*)	BIGNONIEAE: *Callichlamys, Lundia, Mussatia, Pachyptera* (except *P. alliacea*), *Piriadacus, Pleonotoma, Pyrostegia, Potomoganos, Stizophyllum, Tanaecium* (except *T. apiculatum* and *T. nocturnum*), *Roentgenia* (reticulum somewhat spinulose). TECOMEAE: *Argylia, Cybistax, Godmania, Campsis, Campsidium, Paratecoma, Tabebuia, Tecoma, Zeyheria* (also all Old World genera except some species of *Incarvillea* and *Stereospermum*) CRESCENTIEAE: *Parmentiera, Crescentia alata* SCHLEGELIEAE: *Schlegelia* (large-flowered species)
Areolate/perisyncolpate	BIGNONIEAE: *Gardnerodoxa, Mansoa* (s.s.), *Memora flavida, M. pedunculata, M. cristicalyx, M. imperatoris-maximilianii* TECOMEAE: *Delostoma, Perianthomega, Sparattosperma*
Areolate tetrads	*Catalpa, Chilopsis*
Inaperturate, medium-reticulate	BIGNONIEAE: *Clytostoma binatum, C. pterocalyx, Cydista aequinoctialis* (mostly), *C. potosina, Phryganocydia*
Inaperturate, coarse-reticulate	BIGNONIEAE: *Adenocalymma, Distictella, Distictis, Memora* (except *M. flavida* group), *Pithecoctenium, Tanaecium apiculatum, Clytostoma costatum, C. sciuripabulum, C. uleanum, C. convolvuloides* (interrupted exine)
Stephanocolpate (zonocolpate), coarse-reticulate	BIGNONIEAE: *Amphilophium, Anemopaegma robustum, A. insculptum, Glaziovia, Haplolophium, Urbanolophium.*
3-colpate, coarse-reticulate	*Martinella*
Polyporate, finely reticulate	*Amphitecna*
Polyporate, coarse-reticulate	*Tanaecium nocturnum*
Spiroaperturate	*Neojobertia*
Pericolpate (pantocolpate)	*Anemopaegma* (mostly), *Cydista decorum, C. lilacina, C. diversifolia, C. aequinoctialis* (in part), *Pachyptera alliacea*
Spinulose, inaperturate	*Cydista heterophylla* (several unrelated species of other genera—*Phryganocydia, Roentgenia, Adenocalymma, Cyclostoma, Memora*—also show tendency in this direction)
Polyporate, complex exine patterns	*Macranthisiphon, Saritaea*
Ecolpate, 3-porate	*Schlegelia* (small-flowered species)

Not examined: *Romeroa, Ekmanianthe, Synapsis.*



FIGURES 10–18. Tricolpate, finely reticulate Bignoniaceae pollen.—10. *Tabebuia rigida* (Tecomeae), equatorial view.—11. *Spathodea campanulata* (Tecomeae), equatorial view.—12. *Oroxylum indicum* (Oroxyleae), subequatorial view.—13. *Pachyptera standleyi* (Bignonieae), equatorial view.—14. *Parmentiera macrophylla* (Crescentieae), equatorial view.—15. *Ophiocolea floribunda* (Coleeae), equatorial view.—16. *Argylia robusta* (Tecomeae), polar view.—17. *Pachyptera parvifolia* (Bignonieae), polar view.—18. *Pachyptera parvifolia* (Bignonieae), exine closeup. Lines in all figures, except Fig. 18, equal 10 μm. Line in Fig. 18 equals 1 μm.

types in New World Tecomeae; two additional types occur in Old World species of Tecomeae, inaperturate (or monocolpate?) in two species of *Stereospermum* (Ferguson & Santisuk, 1973) and stephanocolpate and subspinulose in *Incarvillea* (Fig. 21).

3-COLPATE, FINELY RETICULATE

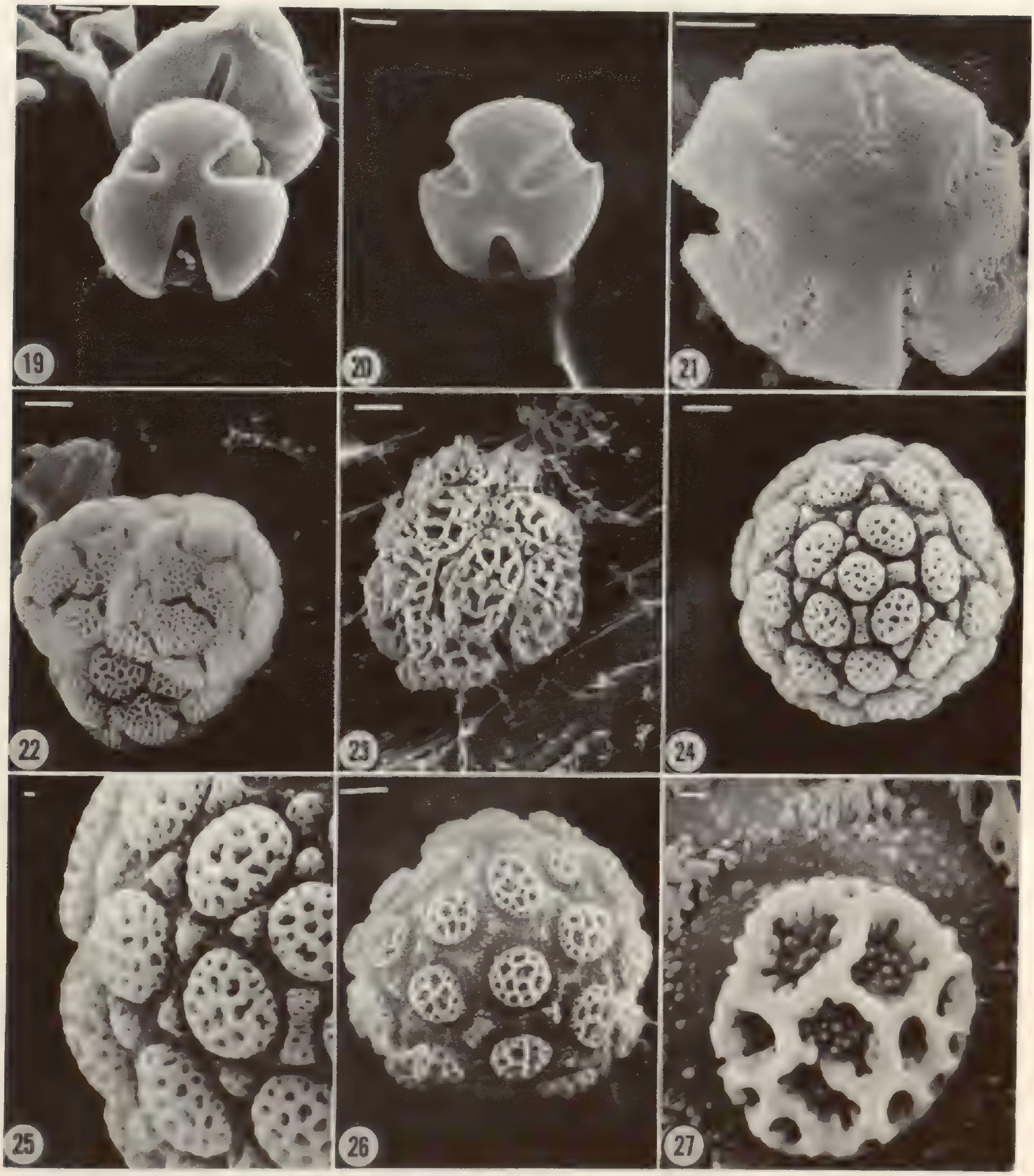
This is the most widespread pollen type in Bignoniaceae and in Tecomeae. Nearly all the Old World species have 3-colpate, finely reticulate pollen (e.g., *Spathodea,* Fig. 11) and have been studied in detail by Buurman (1977). The largest neotropical genus, *Tabebuia,* also has 3-colpate, finely reticulate pollen (Fig. 10). The uniformity of pollen in morphologically heterogeneous *Tabebuia* supports its retention as a single genus and argues against persistent attempts (e.g., Mattos, 1970) to segregate simple-leaved from palmately compound-leaved species or the species with irregularly ridged capsules (*Roseodendron*) from the ones with smooth capsules. Even segregate genera adequately justified on other grounds—*Godmania, Paratecoma, Zeyhera* and *Cybistax*—are palynologically indistinguishable. *Tecoma,* mostly Andean and with pinnately compound leaves, has similar pollen, as do north-temperate *Campsis,* south-temperate *Campsidium,* and all Old World genera, except some species of *Stereospermum* and *Incarvillea. Astianthus,* traditionally but erroneously placed in Bignonieae, also goes here. *Argylia,* the herbaceous genus of the southern Andes has this type of pollen (Fig. 16), although the colpi of some species are operculate with the pollen thus appearing 6-geminicolpate (see also Gleisner & Ricardi, 1969). The pollen of *Argylia* is thus quite unlike that of *Incarvillea* (Fig. 21), the herbaceous Himalayan genus with which it is often compared, and suggests that these two genera (and their sometimes segregates *Oxymitus, Amphicome,* and *Niedzwedskia*) represent convergence rather than a phytogeographical conundrum. Buurman (1977), whose main focus was on this pollen type, recognized five subtypes based on lumina index (ratio of equatorial to polar lumina diameters); we find this character intragenerically variable and of little taxonomic significance at the generic level.

3-COLPATE, PSILATE

The closely related but otherwise very isolated South American genera with elongated staminodes—*Jacaranda* (Fig. 20), centered in central and eastern Brazil, and *Digomphia* (Fig. 19) of Guayana—share an almost psilate, 3-colpate pollen. Thus pollen adds nothing to the rather weak evidence supporting segregation of *Digomphia* but emphasizes the isolation of *Jacaranda* and *Digomphia* from other Tecomeae.

AREOLATE (MODIFIED PERISYNCOLPATE; CAMPORETICULATE)

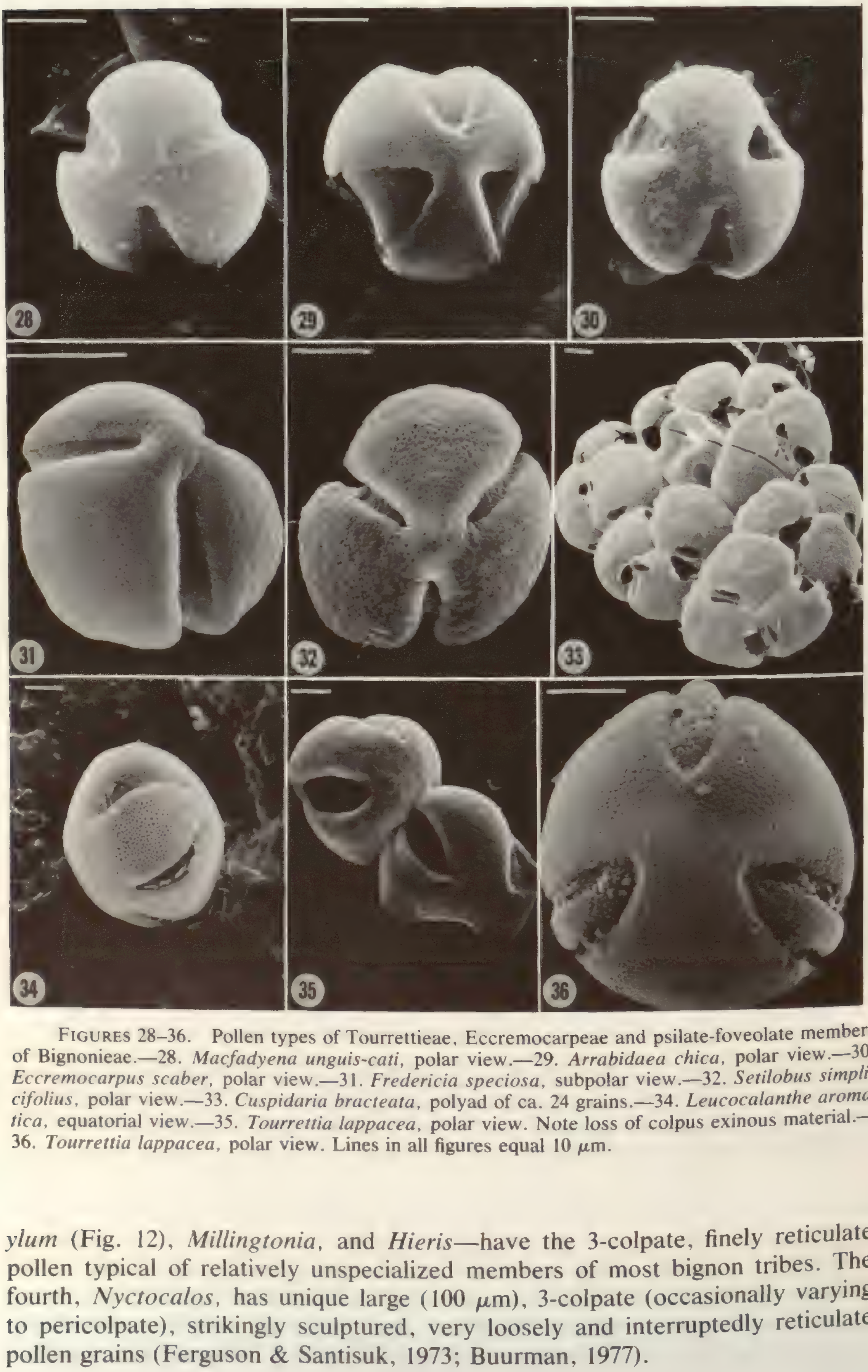
The basically north-temperate genera *Catalpa* (Fig. 22) and *Chilopsis* (Fig. 23) have areolate or camporeticulate pollen aggregated into tetrads. Two South American genera—*Sparattosperma* (Fig. 9), a monotypic cerrado and dry forest plant with palmately compound leaves, and *Delostoma* (Figs. 24–27), an Andean genus with simple leaves—have single-grained areolate pollen. At least in the case of *Sparattosperma,* which shares an unusual seed wing of fused hairs with *Catalpa,* a relationship to the north-temperate genus is suggested. Interestingly, in the Old World genus *Stereospermum* areolate pollen occurs along with 3-colpate and inaperturate (possibly also monocolpate) pollen (Fergusen & Santisuk, 1973; Buurman, 1977) proving that these differences are not necessarily taxonomically fundamental ones, at least at the generic level.



FIGURES 19–27. Palynological variations in Tecomeae—psilate, stephanocolpate, and areolate pollen types.—19. *Digomphia laurifolia*, tricolpate psilate, polar view.—20. *Jacaranda irwinii*, tricolpate psilate, polar view.—21. *Incarvillea emodii*, stephanocolpate, subspinulose.—22. *Catalpa speciosa*, tetrad of areolate grains.—23. *Chilopsis linearis*, tetrad of areolate grains.—24. *Delostoma lobbii*, areolate grain.—25. *Delostoma lobbii*, surface of areolate grain.—26. *Delostoma integrifolium*, areolate grain.—27. *Delostoma integrifolium*, surface of areolate grain. Lines in all figures, except Figs. 25 and 27, equal 10 μm. Lines in Figs. 25 and 27 equal 1 μm.

OROXYLEAE

Four small genera (three monotypic, the fourth with only three species) of southeast Asian trees and nontendrillate climbers with fruit dehiscence parallel to the septum have usually been included in Bignonieae. Three of these—*Orox-*



FIGURES 28–36. Pollen types of Tourrettieae, Eccremocarpeae and psilate-foveolate members of Bignonieae.—28. *Macfadyena unguis-cati*, polar view.—29. *Arrabidaea chica*, polar view.—30. *Eccremocarpus scaber*, polar view.—31. *Fredericia speciosa*, subpolar view.—32. *Setilobus simplicifolius*, polar view.—33. *Cuspidaria bracteata*, polyad of ca. 24 grains.—34. *Leucocalanthe aromatica*, equatorial view.—35. *Tourrettia lappacea*, polar view. Note loss of colpus exinous material.—36. *Tourrettia lappacea*, polar view. Lines in all figures equal 10 μm.

ylum (Fig. 12), *Millingtonia*, and *Hieris*—have the 3-colpate, finely reticulate pollen typical of relatively unspecialized members of most bignon tribes. The fourth, *Nyctocalos*, has unique large (100 μm), 3-colpate (occasionally varying to pericolpate), strikingly sculptured, very loosely and interruptedly reticulate pollen grains (Ferguson & Santisuk, 1973; Buurman, 1977).

BIGNONIEAE

The largest and palynologically most diverse tribe of Bignoniaceae, Bignonieae are restricted to the neotropics (Gentry, 1979a, 1979b) with a single outlier, *Bignonia capreolata,* in the southeastern United States. The 500 species are mostly lianas and the poorly defined genera are mostly responsible for the bad taxonomic reputation of the family. Palynology has already contributed much to the taxonomy of this tribe (Urban, 1916; Gomes, 1955), and the availability of the SEM provides additional useful information. Seven major palynological categories can be recognized in this tribe, three of them corresponding to the pollen types already listed above for Tecomeae.

3-COLPATE, FINELY RETICULATE

A rather diverse group of genera centering around *Pyrostegia* have pollen similar to that characteristic of most Tecomeae. These include *Pyrostegia* (Fig. 3) (1 species in part 4-colpate), *Roentgenia* (ca. 4-colpate) (Figs. 44–45), *Potomoganos, Lundia, Mussatia, Piriadacus, Callichlamys, Pleonotoma* (including *Nestoria*), *Stizophyllum, Pachyptera* (Figs. 17–18) (including *Pseudocalymma*), and *Tanaecium* (but excluding *T. nocturnum* and *T. apiculatum*). These genera are probably not closely related, although their pollen presumably represents an ancestral type shared with most Tecomeae. *Roentgenia* differs somewhat in a tendency to subverrucate sculpturing of the exine.

3-COLPATE, PSILATE

Most species of Bignonieae have 3-colpate, more or less psilate, usually microperforate, pollen. The following subgourps are recognizable:

(1). Simple tendrils and (usually) pubescent corolla tubes with white to magenta flowers characterize a large group of traditionally recognized genera centering around *Arrabidaea* which share 3-colpate more or less psilate pollen. Many of these genera are monotypic and merger of at least some of them with *Arrabidaea* has been suggested (Gentry, 1977a, 1977b; Sandwith, 1968). Besides *Arrabidaea* (Fig. 29) (including *Cremastus, Petastoma, Scobinaria, Neomacfadya, Paramansoa,* etc.), these genera include *Xylophragma* (Fig. 1) (including *Orthotheca,* see Gentry, following paper), *Fridericia* (Fig. 31), *Setilobus* (Fig. 32) (listed as stephanocolpate by Buurman), *Pseudocatalpa,* and *Cuspidaria* (Fig. 2) (including *Saldanhaea* and *Blepharitheca*). *Cuspidaria* differs from the others in pollen aggregated into tetrads, unique in Bignonieae. One species, *C. bracteata* (Fig. 33), has polyads, previously unreported in the family and making Bignoniaceae the eighth known polyad-containing angiosperm family (cf. Walker & Doyle, 1975).

(2). A number of small genera with more or less psilate 3(–4)–colpate pollen, pubescent corolla tubes and (2–)3(–multi)-fid (but never uncate, sometimes in part undivided) tendrils form a probably natural group. These include *Periarrabidaea, Leucocalanthe* (4–5-colpate) (Fig. 34), *Spathicalyx* [including "*Arrabidaea*" *xanthophylla* (Gentry, 1977c)], *Manaosella, Ceratophytum, Tynnanthus,* and *Paragonia* (including *Sanhilaria*).

(3). Genera with uncate "cat's claw" tendrils and glabrous corolla tubes make

up a third group, centering around *Macfadyena*, with psilate 3-colpate pollen (Fig. 28). These include *Macfadyena* (including *Doxantha*), *Melloa*, *Dolichandra*, *Parabignonia* (one of the two species with minutely puberulous upper corolla tube), and *Paradolichandra*. Inclusion here of the last three genera, traditionally included in Tecomeae because their capsule dehiscence is (supposedly) perpendicular to the septum, is noteworthy. Morphologically they are very close to the *Macfadyena* alliance and completely out of place in Tecomeae. That their pollen is the same as in morphologically similar *Macfadyena*, but matched in Tecomeae only by utterly different *Jacaranda* and *Digomphia*, supports their placement in Bignonieae. Moreover, only *Dolichandra* has fruit dehiscence consistently perpendicular to the septum and even here some fruits are 4-valved and thus both perpendicular and parallel to the septum.

3-COLPATE, COARSE-RETICULATE

Only the single genus *Martinella* (Fig. 4) is known to have this type of pollen.

STEPHANOCOLPATE (ZONOCOLPATE), COARSE-RETICULATE

A natural group of small, closely related genera centering around *Amphilophium—Amphilophium* (Figs. 7–8), *Haplolophium*, *Glaziovia*, *Urbanolophium*—has this distinctive pollen type. All these genera are characterized by a frilly outer calyx margin, unique in the family. A few species of *Anemopaegma*, notably *A. insculptum* and *A. robustum*, are stephanocolpate and have a relatively coarse reticulum, thus palynologically approaching this group.

INAPERTURATE, COARSE-RETICULATE

There are two probably unrelated groups of genera with inaperturate, coarse-reticulate pollen.

(1). Thick-textured white to purple or red flowers, trifid (–multifid) tendrils, and multi-seriate ovules and seeds characterize a group centering around *Pithecoctenium* (Fig. 54) and including also *Distictella* (Fig. 6) and *Distictis* (including *Phaedranthus*, *Wunschmannia*, *Macrodiscus*, and *Anomoctenium*, Gentry, 1974d). *Neves-armondia* should be reduced to *Pithecoctenium* (see Gentry, following paper).

(2). Medium-textured yellow (rarely white or orangish) flowers, simple tendrils and mostly 2-seriate ovules and seeds characterize an assemblage including *Adenocalymma* (Figs. 48–49), most species of *Memora* (Fig. 46), and two of *Tanaecium*. This is certainly a basically natural group and *Memora* could readily be merged with *Adenocalymma* if the not-always-constant definitive character of pinnately compound versus 3-foliolate or 2-foliolate leaves were neglected. *Tanaecium* may be an artificial assemblage based on independent evolution for hawk-moth pollination but more evidence is needed; *T. apiculatum* may be a hawk-moth pollinated derivative of *Adenocalymma* to judge from its pollen; *T. nocturnum* (*Osmohydrophora*) (Figs. 52–53) differs palynologically from other species assigned here in having noticeable pores though lacking colpi.

INAPERTURATE MEDIUM-RETICULATE

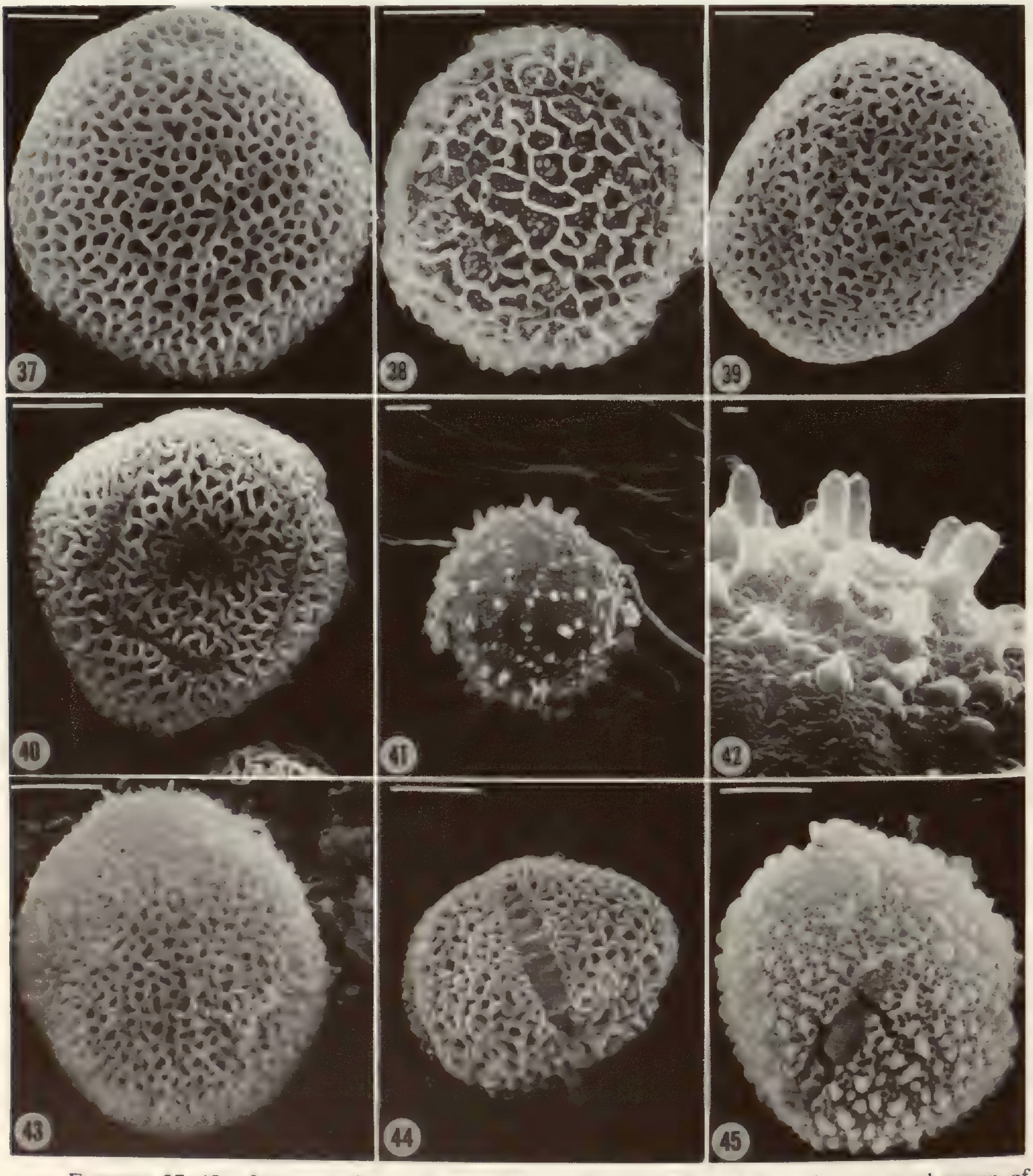
The genera which lack nectariferous discs and favor "multiple bang" flowering phenologies (Gentry, 1974a, 1974b) mostly have inaperturate, medium-reticulate pollen and apparently constitute a natural group, which includes *Clytostoma* (Figs. 37–38), *Phryganocydia* (Fig. 43), and most species of *Cydista* (Figs. 5, 39) (including *Levya*). All have thin magenta (or white) corollas, simple tendrils, and 8–16 phloem arms in cross-section. Three species of *Cydista*—*C. decora, C. lilacina,* and *C. diversifolia* (Fig. 40)—have a similar reticulum but are pericolpate and may represent an intermediate stage with related colpate genera. *Cydista aequinoctialis* may be either pericolpate or inaperturate. *Cydista heterophylla* (Figs. 41–42) is inaperturate but has a unique spinulose exine and apparently is palynologically derived but related. *Roentgenia* (Figs. 44–45), which is morphologically very close to *Cydista* (except for the minutely trifid tendrils), has a similar (though more verrucate or scabrate) pollen reticulum but the grains are colpate; its segregation, and that of 3-colpate monotypic *Potomoganos*, is justified mostly by the palynological difference.

AREOLATE/PERISYNCOLPATE

A number of genera of Bignonieae have areolate pollen similar to *Sparattosperma* and *Delostoma* of the Tecomeae. This does not appear to be a natural alliance and consists of at least three distantly related subgroups.

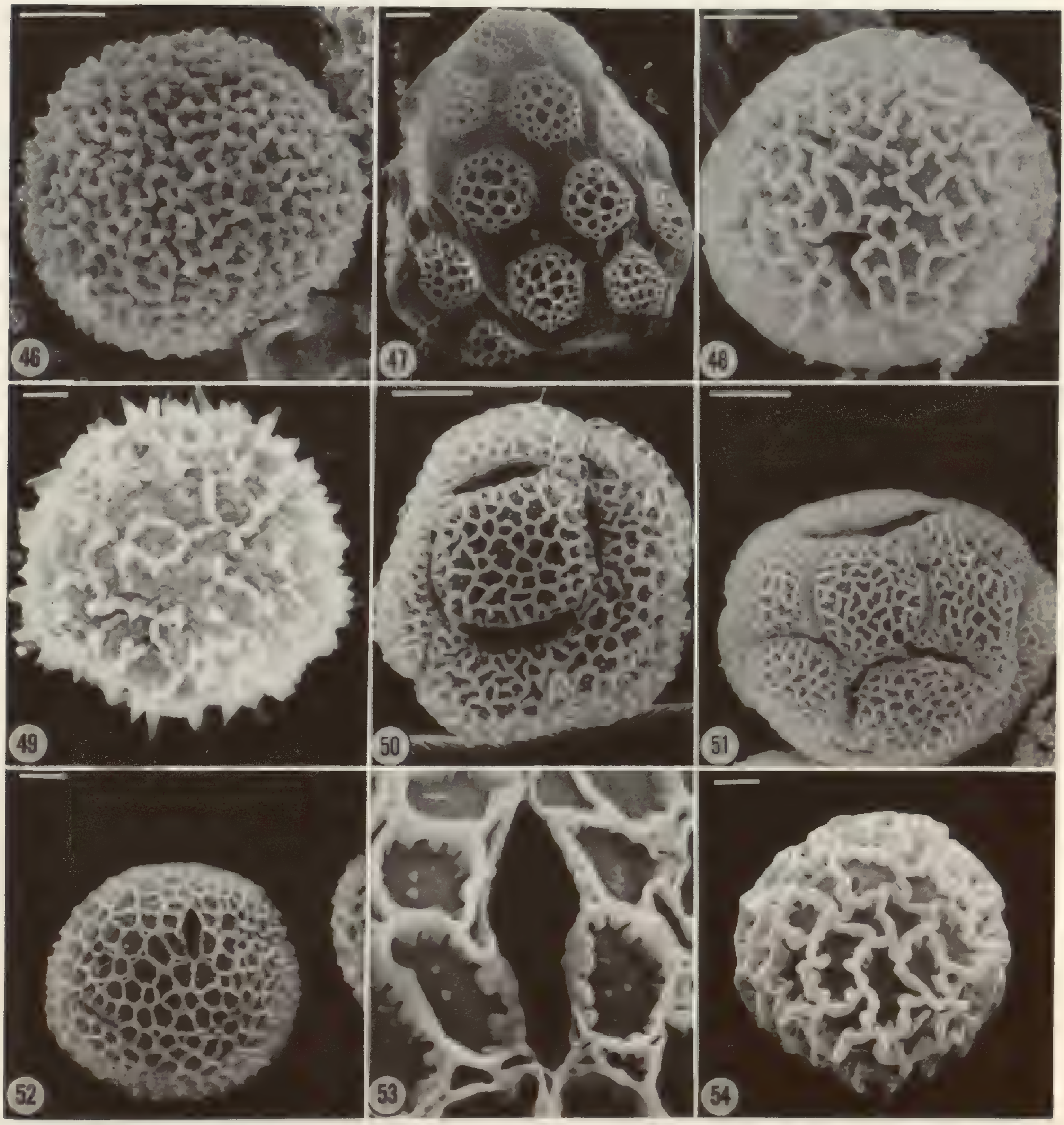
(1). Trifid tendrils and magenta puberulous corollas characterize a natural group of genera, including *Mansoa* and its allies *Gardnerodoxa* and *Onohualcoa*. *Onohualcoa* has already been lumped with *Mansoa*, largely on the basis of the palynological evidence (Gentry, 1976c). *Hanburyophyton* (Fig. 51) should also be reduced to *Mansoa* (see following paper). Interestingly, *Pachyptera alliacea* (Fig. 50) has perisyncolpate pollen (with less pronounced nonreticulate areas) and provides a significant connection between *Mansoa* and the other two onion-smelling species of *Pachyptera* (Fig. 13) which are 3-colpate. These three onion-smelling species are so closely related that Sandwith (1954) considered all three conspecific. *Pachyptera* (Figs. 13, 17–18) is closer to *Mansoa* than to any other genus despite the palynological difference. Three *Cydista* species—*C. diversifolia, C. decora,* and *C. lilacina*—also have pericolpate pollen as noted above and may connect mostly inaperturate *Cydista* to the *Mansoa* alliance.

(2). *Anemopaegma* and its allies have cream or yellow flowers with a characteristic shape, trifid or simple tendrils, and a very characteristic stipitate ovary and flattened oblong-stipitate fruit. The pollen of most species is pericolpate to perisyncolpate with the fairly coarse-reticulate exine interrupted by narrow, often interrupted, colpi. The exine of some species of *Anemopaegma* approaches that of *Amphilophium* and its allies but the two groups are not closely related. *Pseudopaegma* was segregated from *Anemopaegma* mainly on accout of its 5–6-colpate pollen, whereas *Anemopaegma* was characterized as inaperturate (Urban, 1916). As the SEM makes obvious, the pollen of most species of *Anemopaegma* is actually inconspicuously perisyncolpate, and *Pseudopaegma* should be reduced to synonymy (Gentry, 1976c).



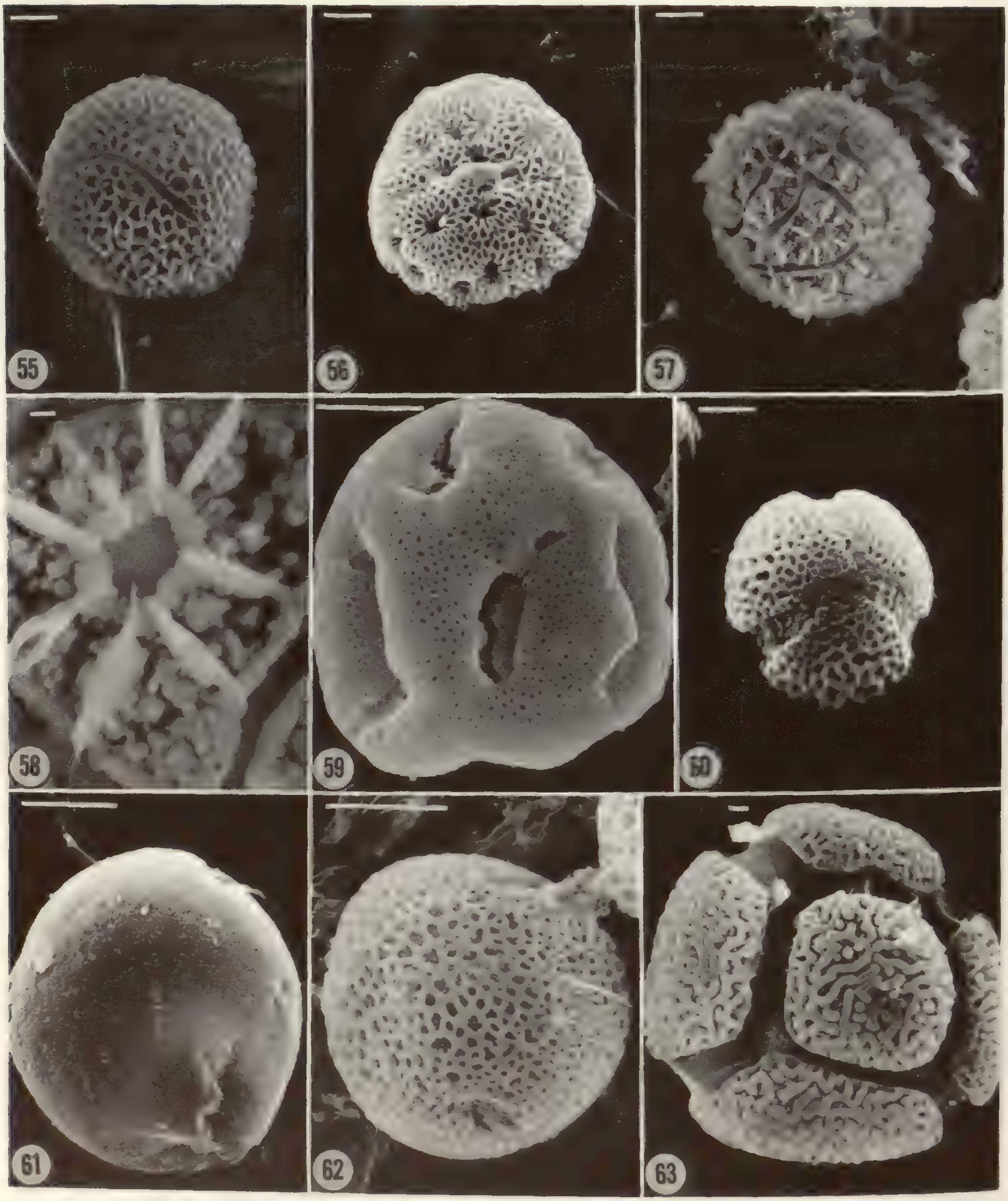
FIGURES 37–45. Intrageneric and intergeneric palynological variations in a natural group of Bignonieae—inaperturate, medium-reticulate pollen types and presumably related pollen types of morphologically allied species.—37. *Clytostoma binatum*, inaperturate, medium-reticulate.—38. *Clytostoma uleanum*, inaperturate, coarse-reticulate.—39. *Cydista potosina*, inaperturate, medium-reticulate.—40. *Cydista diversifolia*, pericolpate, medium-reticulate.—41. *Cydista heterophylla*, inaperturate, spinulose.—42. *Cydista heterophylla*, exine close up.—43. *Phryganocydia corymbosa*, inaperturate, scabrate.—44. *Roentgenia sordida*, colpate, scabrate.—45. *Roentgenia bracteomana*, colpate, verrucate. Lines in all figures, except Fig. 42, equal 10 μm. Line in Fig. 42 equals 1 μm.

(3). Several species of *Memora*—*M. alba* (Aubl.)Miers, *M. flavida* (DC.)Bur. & K. Schum., *M. pedunculata* (Fig. 47) and several poorly known species from northeastern Brazil—have areolate pollen rather than the continuous exine characteristic of most of the genus. The tendrils are trifid in *M. flavida* and *M. alba*,



FIGURES 46–54. Palynological variations in Bignonieae—coarse-reticulate inaperturate and areolate pollen types.—46. *Memora campicola*.—47. *Memora pedunculata*.—48. *Adenocalymma bracteatum*.—49. *Adenocalymma inundatum*.—50. *Pachyptera alliacea*.—51. *Mansoa lanceolata* (*Hanburyophyton xanthinum*).—52. *Tanaecium nocturnum*.—53. *Tanaecium nocturnum*.—54. *Pithecoctenium crucigerum*. Lines in all figures, except Fig. 53, equal 10 μm. Line in Fig. 53 equals 1 μm.

unique in the genus, but are not known in the other areolate species. These species also have paniculate rather than racemose inflorescences. If the northeastern Brazilian species *M. cristicalyx* A. Gentry and *M. imperatoris-maximilianii* (Wawra)A. Gentry prove to have trifid tendrils, this group might well merit generic recognition. At present, it is best retained as a well-marked section of *Memora*. *Perianthomega vellozoi* (Fig. 63), which is one of the most isolated species of the family, is probably related to this group on account of its areolate pollen and bicompound leaves.



FIGURES 55–63. Miscellaneous pollen types of neotropical Bignoniaceae.—55. *Neojobertia candolleana* (Bignonieae), spiroaperturate.—56. *Macranthisiphon longiflorus* (Bignonieae), polyporate, medium-reticulate.—57. *Saritaea magnifica* (Bignonieae), polyporate, irregularly spiroaperturate, complexly reticulate.—58. *Saritaea magnifica* (Bignonieae), exine close-up.—59. *Amphitecna latifolia* (Crescentieae), polyporate, psilate-foveolate.—60. *Schlegelia nicaraguensis* (Schlegelieae), tricolpate, medium-reticulate.—61. *Schlegelia fastigiata* (Schlegelieae), triporate, psilate-foveolate.—62. *Schlegelia pandurata* (Schlegelieae), triporate, medium-reticulate.—63. *Perianthomega vellozoi* (Tecomeae?), striate, areolate. Lines in all figures, except Fig. 58, equal 10 μm. Line in Fig. 58 equals 1 μm.

MISCELLANEOUS

Neojobertia candolleana (Fig. 55) has a unique spiroaperturate pollen grain, though somtimes described as areolate (i.e., camporeticulate, Gomes, 1955) or considered operculate-tricolpate (Buurman, 1977). Its unique pollen supports its status as a well-defined monotypic genus.

Saritaea (Figs. 57–58) has been widely remarked for its unique, polyporate and irregularly spiroaperturate, complexly reticulate exine with thickened muri radiating out from the apertures and enclosing granular-spinulose, wedge-shaped lumina (Ferguson & Santisuk, 1973; Buurman, 1977). The only remotely similar pollen type in the family is that of *Macranthisiphon* (Fig. 56) which is polyporate with muri radiating out from the pores and enclosing wedge-shaped lumina but a much more regular evenly reticulate sexine. While the palynological evidence strongly supports retention of both these monotypic genera, it also suggests that *Saritaea* might be derived from a *Macranthisiphon*-like ancestor. There is no reason whatsoever to suppose that the complex, highly advanced pollen of *Saritaea* has given rise to the more prevalent, 3-colpate types as suggested by Suryakanta (1973).

Eccremocarpeae and Tourrettieae

The pollen of both of these small and isolated monogeneric tribes is psilate and 3-colpate, thus similar to *Jacaranda* and *Digomphia* of the Tecomeae and to many genera of Bignonieae. The similarity of pollen between *Eccremocarpus* (Fig. 30) and *Jacaranda* could be interpreted to support Bentham & Hooker's (1876) long discredited treatment of these two genera as belonging to the same tribe but the prevalence of this pollen type in various unrelated groups of Bignonieae suggests that it may have little taxonomic significance at the tribal level. *Tourrettia* (Figs. 35–36) is highly anomalous in Bignoniaceae, but its pollen is not out of place, despite the tectate colpi.

Crescentieae

This tribe should be restricted to the indehiscent-fruited neotropical species of Bignoniaceae (Gentry, 1976b, 1979b). There are three genera with as many basic pollen types and even intraspecific variation has been reported (Buurman, 1977). *Parmentiera* (Fig. 14) has small-reticulate, 3-colpate pollen similar to that of most species of Tecomeae. *Amphitecna* (Fig. 59) (including *Enallagma* and *Dendrosicus*, Gentry, 1976a) has ecolpate, finely reticulate, multiporate pollen. *Crescentia cujete* has been reported as ecolpate (Urban, 1916) but is actually 6-colpate, having three primary colpi each interrupted equatorially; it is thus palynologically intermediate between *Parmentiera* and *Amphitecna*. *Crescentia alata* with a similar exine to that of *C. cujete* but 3-colpate pollen is not essentially different from *C. cujete*, and its segregation as *Pteromiscus* (Pichon, 1945) is unjustified, even palynologically.

Coleeae

The five genera of indehiscent-fruited Madagascar Bignoniaceae (and *Kigelia* of continental Africa) evolved from a different ancestral stock of Tecomeae than

did the neotropical Crescentieae so must be taxonomically separated as tribe Coleeae (Gentry, 1976b). All species which have been examined have the 3-colpate, finely reticulate pollen (e.g., *Ophiocolea,* Fig. 15) typical of unspecialized representatives of most of the other tribes of the family.

SCHLEGELIEAE

Schlegelia and its allies constitute a problematical group intermediate between Bignoniaceae and Scrophulariaceae. As these species have indehiscent, berrylike fruits, they are often placed in Crescentieae but clearly warrant tribal segregation (Gentry, 1979b). Whether Schlegelieae belong in Bignoniaceae or Scrophulariaceae remains unresolved. Symptomatic of the familial problem is the newly described Central American genus *Gibsoniothamnus* (Williams, 1970). Described in Scrophulariaceae to include three species described as Verbenaceae, it was soon discovered that one of these "Verbenaceae" species had previously been described as Bignoniaceae (Gentry, 1971). Specimens of one Panamanian species of *Gibsoniothamnus* were discovered as "indets" referred to five different families (Verbenaceae, Scrophulariaceae, Bignoniaceae, Gentianaceae and Solanaceae) (Gentry, 1974e)! *Schlegelia* itself was described twice, first as Gesneriaceae (later transferred to Bignoniaceae) and then as *Dermatocalyx* of Scrophulariaceae; that these two genera are identical was not discovered until 1949. Another *Schlegelia* species was recently discovered to belong in Boraginaceae (Gentry, 1973).

Pollen of *Schlegelia* (Figs. 60–62) and its relatives is somewhat heterogeneous but of two main types. The large-flowered speices of *Schlegelia* [*S. nicaraguensis* (Fig. 60), *S. dressleri*] have 3-colpate, finely reticulate pollen similar to that of most Tecomeae and many Bignonieae but with apparently operculate colpi. Small-flowered species of *Schlegelia* have ecolpate, 3-porate pollen with either a psilate (*S. fastigiata,* Fig. 61) or medium-reticulate (*S. pandurata,* Fig. 62) exine. This palynological dichotomy supports the suggestion (Gentry, 1974c) that *Schlegelia* may constitute two genera, the large-flowered species assignable to Bignoniaceae and the small-flowered ones possibly belonging to Scrophulariaceae. *Gibsoniothamnus* has subpsilate 3-colpate pollen with short colpi and might thus be interpreted as palynologically intermediate between the subpsilate 3-porate species of *Schlegelia* and the more widespread psilate 3-colpate pollen type.

CONCLUSIONS

Although pollen of Bignoniaceae is indeed heterogeneous, most of the pollen types of the family have evolved independently in several evolutionary lineages, suggesting that these palynological differences may be less fundamental than often supposed. For example, areolate pollen occurs independently in tribes Tecomeae and Bignonieae and repeatedly in unrelated groups within each tribe. Inaperturate pollen has also evolved in several unrelated genera and in both major tribes, and tetrads occur in both major tribes.

Nevertheless, palynological differences are taxonomically very important if correctly interpreted, and most genera are characterized by a single pollen type. We may generalize that certain kinds of intrageneric palynological variation are

allowable, although even the most eurpalynous genera show a single well-developed palynological trend. Thus the change from 3-colpate to perisyncolpate to multiporate to inaperturate in *Tanaecium* (Tomb & Gentry, in prep.) reflects a single evolutionary theme. In *Cydista* the trend is from perisyncolpate to inaperturate with one species—*C. heterophylla*—losing most of its exine reticulation as well as becoming rather spinulose. In the *Pachyptera/Mansoa* alliance we have 3-colpate species in *Pachyptera* and areolate species in *Mansoa* but perisyncolpate *P. alliacea* is intermediate. Reduction of sculpturing of the exine to an irregular, more or less spinulose texture has happened repeatedly in unrelated genera and appears of little taxonomic significance above the species level. On the other hand, the size of exine reticulation appears more conservative than number and type of colpi and is very useful in generic definition. The only genus with significant variation in exine reticulation size is *Clytostoma,* which is uniformly inaperturate but varies from medium reticulate to coarsely reticulate.

The finely reticulate, 3-colpate type of pollen is almost certainly the ancestral or basal type in the family. This can be inferred both from its broad distribution across all tribes and in all geographic regions and from its prevalence in each tribe in taxa regarded as less specialized on morphological grounds. Moreover, in the context of the family as a whole this putatively unspecialized pollen type is most common in the morphologically less advanced Tecomeae and Oroxyleae. The interpretation of finely reticulate, 3-colpate pollen as primitive in Bignoniaceae is in broad agreement with the conclusions of Buurman (1977). However, her additional suggestion that within the 3-colpate palynological group, the smooth-exined *Arrabidaea* type gives rise to the finely reticulate *Tecoma* type is not supported, since the former is restricted to several largely unrelated groups of the specialized tribe Bignonieae and the highly derived genus *Jacaranda* (and its segregate *Digomphia*) in Tecomeae. It seems far more likely that opposite trends toward psilate and coarsely reticulate exines both originated from similar finely reticulate ancestral types.

This survey of Bignoniaceae pollen confirms its taxonomic importance in generic delimitation and suggests that pollen may be equally useful for grouping related genera at the subtribal level. On the other hand, pollen is of minimal taxonomic use at the tribal and familial level in Bignoniaceae. The genera and informal generic groupings proposed here are consistent with all available evidence, palynological as well as morphological, and mostly constitute unarguably natural groups. That the very palynological data which previously have been used to support excessive generic splitting have proven to support larger natural genera and generic groupings is particularly gratifying.

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APPENDIX: Species examined.

Adenocalymma inundatum Mart. ex DC.	*Woodson et al. 1578* (MO)
A. bracteatum (Cham.) DC.	*Williams 7391* (MO)
Amphilophium paniculatum (L.) H.B.K.	*Blum 1258* (MO)
Amphitecna latifolia (Mill.) A. Gentry	*Dwyer 1568* (MO)
A. sessilifolia (Donn. Sm.) L. Wms.	*Wilbur & Stone 9867* (MO)
A. megalophylla (Donn. Sm.) A. Gentry	*Wilson 274* (F)
A. montana L. Wms.	*Breedlove 25718* (MO)
Anemopaegma arvense (Vell.) Stellf. ex de Souza	*Hatschbach 27921* (MO)
A. chrysoleucum (H.B.K.) Sandw.	*Gentry 3848* (MO)
A. insculptum (Sandw.) A. Gentry	*Prance et al. 14704* (MO)
A. alatum A. Gentry	*Steyermark et al. 107753* (MO)
A. orbiculatum (Jacq.) DC.	*Gentry 2820* (MO)
A. robustum Bur. & K. Schum.	*de la Cruz 3000* (MO)
Argylia potentillaefolia DC.	*Wagenknecht 18582* (MO)
A. robusta Sandw.	*Senn 4343* (MO)
Arrabidaea bilabiata (Sprague) Sandw.	*Lleras et al. P17164* (MO)
A. chica (H. & B.) Verl.	*Gentry 7766* (MO)
A. elegans (Vell.) A. Gentry	*Mello s.n.* (RB-43228) (MO)
A. florida DC.	*Gentry 1605* (MO)
A. inaequalis (DC. ex Splitg.) K. Schum.	*Rutkis 211* (VEN)
A. podopogon (DC.) A. Gentry	*Gentry 8056* (MO)
A. prancei A. Gentry	*Prance et al. 13757* (MO)
A. sceptrum (Cham.) Sandw.	*Irwin et al. 16163* (MO)
A. triplinervia (DC.) Baill. ex Bur.	*Prance et al. 14292* (MO)
A. verrucosa (Standl.) A. Gentry	*Gentry 7988* (MO)
Astianthus viminalis (H.B.K.) Baill.	*Hinton 9972* (MO)
Bignonia capreolata L.	*Bush 2270* (MO)
Callichlamys latifolia (L. Rich.) K. Schum.	*Gentry 1896* (MO)
Campsidium valdivianum (Phil.) Skottsb.	*Werdermann 74* (MO)
Catalpa speciosa (Ward. ex Barney) Engelm.	*Palmer 30318* (MO)
Ceratophytum tetragonolobum (Jacq.) Sprague & Sandw.	*Tun 993* (MO)
Chilopsis linearis (Cav.) DC.	*Eggers s.n.* (MO)
Clytostoma binatum (Thunb.) Sandw.	*Gentry 5127* (MO)
C. convolvuloides Bur. & K. Schum.	*St. Hilaire s.n.* (P)
C. costatum Bur. & K. Schum.	*Carauta 279* (GUA)
C. pterocalyx Sprague ex Urb.	*Gentry et al. 11032* (MO)
C. sciuripabulum Bur. & K. Schum.	*Gentry 12513* (MO)
C. uleanum Kränzl.	*Chavez 451* (MO)
Crescentia alata H.B.K.	*Wilbur & Stone 1768* (MO)
C. cujete L.	*Gentry 3690* (MO)
Cuspidaria bracteata Bur. ex Baill.	*Glaziou 11225* (P)
C. convoluta (Vell.) A. Gentry	*Hassler 4224* (MO)
C. floribunda (DC.) A. Gentry	*Irwin et al. 25769* (MO)
Cydista aequinoctialis (L.) Miers	*Gentry & Tyson 5758* (MO); *Maguire 24700* (MO)
C. decora (S. Moore) A. Gentry	*Camp 3812* (MO); *Hassler 10022a* (MO)
C. diversifolia (H.B.K.) Miers	*Webster et al. 12722* (MO)
C. heterophylla Seib.	*Gentry 4967* (MO)
C. lilacina A. Gentry	*Gentry et al. 10673* (MO)
C. potosina (K. Schum. & Loes.) Loes.	*Tun 1211* (MO)
Delostoma lobbii Seem.	*Hutchinson et al. 6201* (MO)
D. integrifolium D. Don	*Woytkowski 7776* (MO)
Digomphia laurifolia Benth.	*Cardona 3027* (VEN)
Distictella magnoliifolia (H.B.K.) Sandw.	*Prance 13876* (MO)
Distictis buccinatoria (DC.) A. Gentry	*Boutin 3317* (MO)
D. granulosa Bur. & K. Schum.	*Haught 2209* (MO)
Dolichandra cynanchoides Cham.	*Hassler 12548* (MO)
Dolichandrone spathacea (L.f.) K. Schum.	*Gillis 11104* (MO)

APPENDIX: Continued.

Eccremocarpus scaber R. & P.	*Boelcke 6474* (MO)
Fridericia speciosa Mart.	*Gottsberger 788* (MO)
Gardnerodoxa mirabilis Sandw.	*Castellanos 25315* (GUA)
Gibsoniothamnus latidentatus A. Gentry	*Dwyer et al. 7293* (MO)
G. mirificus A. Gentry	*Wiehler s.n.* (MO)
Glaziovia bauhinioides Bur. ex Baill.	*Duarte s.n.* (RB-166032) (MO)
Godmania aesculifolia (H.B.K.) Standl.	*Allen 4492* (MO)
Haplolophium bracteatum Cham.	*Sellow s.n.* (US)
Haplophragma adenophyllum (Wall. ex G. Don) Dop	*Gentry 1446A* (MO)
Incarvillea emodii (Lindl.) Chatterjee	*Steward 14637* (MO)
Jacaranda caucana subsp. *sandwithiana* A. Gentry	*Tyson 3463* (MO)
J. irwinii A. Gentry	*Irwin et al. 32250* (MO)
Kigelia africana (Lam.) Benth.	*Gentry 6053* (MO)
Leucocalanthe aromatica Barb. Rodr.	*Ducke 239* (MO)
Lundia corymbifera (Vahl) Sandw.	*Gentry 5565* (MO)
Macfadyena uncata (Andr.) Sprague & Sandw.	*Gentry 8380* (MO)
M. unguis-cati (L.) A. Gentry	*Croat 14031* (MO)
Macranthisiphon longiflorus (Cav.) K. Schum.	*Dodson & Thien 1296* (MO)
Manaosella cordifolia (DC.) A. Gentry	*Hatschbach 31389* (MO)
Mansoa difficilis (Cham). Bur. & K. Schum.	*Marunak 192* (MO)
M. glaziovii Bur. & K. Schum.	*Glaziou 12991* (P)
M. lanceolata (DC.) A. Gentry	*Miers 3080* (P)
M. ventricosa A. Gentry	*Maguire et al. 56083* (MO)
M. verrucifera (Schlecht.) A. Gentry	*Gentry 6527* (MO)
Martinella obovata (H.B.K.) Bur. & K. Schum.	*Croat 14105* (MO)
Melloa quadrivalvis (Jacq.) A. Gentry	*Venturi 9662* (MO)
Memora bipinnata (S. Moore) A. Gentry	*Hatschbach 36033* (MO)
M. campicola Pilger	*Irwin et al. 16477* (MO)
M. magnifica (Mart. ex DC.) Bur.	*Gentry 13164* (MO)
M. patula Miers	*Lasser 4309* (VEN)
M. pedunculata (Vell.) Miers	*Anderson et al. 35210* (MO)
Mussatia hyacinthina (Standl.) Sandw.	*Tun 992* (MO)
Neojobertia candolleana (Mart. ex DC.) Bur.	*Castellanos 25225* (MO)
Ophiocolea floribunda (Boj.) H. Perr.	*Gentry 11360* (MO)
Oroxylum indicum (L.) Vent.	*Saklani s.n.* (MO)
Pachyptera alliacea (Lam.) A. Gentry	*Ducke 22697* (MO)
P. hymenaea (DC.) A. Gentry	*Breedlove 24138* (MO); *Schwacke & Glaziou s.n.* (MO)
P. kerere (Aubl.) Sandw.	*Gentry 7687* (MO)
P. parvifolia A. Gentry	*Berlin 828* (MO)
P. standleyi (Steyerm.) A. Gentry	*Gentry 10899* (MO)
Parabignonia unguiculata (Vell.) A. Gentry	*Blanchet s.n.* (P)
Paradolichandra chodatii Hassler	*Fiebrig 5071* (P)
Paragonia pyramidata (L. Rich.) Bur.	*Croat 8309A* (MO)
Paratecoma peroba (Record) Kuhlm.	*Evangeliste s.n.* (RB-68377) (RB)
Parmentiera aculeata (H.B.K.) Seem.	*Pringle 7524* (MO)
P. macrophylla Standl.	*Lewis et al. 1780* (MO)
Paulownia tomentosa (Thunb.) Steud.	*Allard 6549* (MO)
Perianthomega vellozoi Bur.	*Hassler 7356* (US)
Periarrabidaea truncata A. Samp.	*Gentry 12824* (MO)
Phryganocydia corymbosa (Vent.) Bur. ex K. Schum.	*Duke 8781* (MO)
Piriadacus erubescens (Mart. ex DC.) Pichon	*Belem 3617* (MO)
Pithecoctenium crucigerum (L.) A. Gentry	*Croat 5804* (MO)
P. hatschbachii A. Gentry	*Glaziou 12972* (P)
Pleonotoma albiflora (Salzm. ex DC.) A. Gentry	*Riedel 750* (P)
P. variabilis (Jacq.) Miers	*Croat 5607* (MO)
Potomoganos microcalyx (G. Mey.) Sandw.	*Maguire et al. 29973* (VEN)

APPENDIX: Continued.

Pseudocatalpa caudiculata (Standl.) A. Gentry	*Gentry 7662* (MO)
Pyrostegia dichotoma Miers ex K. Schum.	*Woytkowski 35089* (MO)
P. venusta (Ker.) Miers	*Dusen 15238* (MO)
Rhigozum obovatum Burchell	*Gillett 17487* (MO)
Roentgenia bracteomana (Schum. ex Sprague) Urb.	*Mexia 6320* (MO)
R. sordida (Bur. & K. Schum.) Sprague & Sandw.	*Marcano 199* (VEN)
Saritaea magnifica (Sprague ex v. Steen.) Dugand	*Gentry 6049* (MO)
Schlegelia brachyantha Griseb.	*Wagner 972* (MO)
S. dressleri A. Gentry	*Dressler 3507* (MO)
S. fastigiata Schery	*Porter et al. 4432* (MO)
S. nicaraguensis Standl.	*Lewis et al. 2319* (MO)
S. pandurata (Moldenke) A. Gentry	*Romero C. 5377* (COL)
S. paraensis Ducke	*Ducke s.n.* (RB-17700) (MO)
S. parasitica (Sw.) Miers ex Griseb.	*Burch & Proctor 7117* (MO)
S. parviflora (Oerst.) Monachino	*Gentry 17806* (MO)
S. violacea (Aubl.) Griseb.	*Mori et al. 8018* (MO)
Setilobus simplicifolius K. Schum.	*Guedes 512* (US)
Sparattosperma leucanthum (Vell.) K. Schum.	*Seibert 1898* (MO)
Spathicalyx duckei (A. Samp.) A. Gentry	*Ducke 17137* (MO)
S. xanthophylla (DC.) A. Gentry	*Klug 3410* (MO)
Spathodea campanulata Beauv.	*Croat 8890* (MO)
Stizophyllum riparium (H.B.K.) Sandw.	*Gentry 7603* (MO)
Tabebuia donnell-smithii Rose	*Harmon & Fuentes 5258* (MO)
T. rigida Urb.	*Otero 658* (MO)
T. rosea (Bertol.) DC.	*Gentry 4579* (MO)
T. stenocalyx Sprague & Stapf	*Steyermark 93076* (VEN)
Tanaecium apiculatum A. Gentry	*F. Smith 226* (US)
T. crucigerum Seem.	*Aristeguieta 5514* (VEN)
T. jaroba Sw.	*Hassler 7384* (P)
T. nocturnum (Barb. Rodr.) Bur. & K. Schum.	*Bristan s.n.* (MO)
Tecoma garrocha Hieron.	*Jörgensen 995* (MO)
T. stans (L.) Juss. ex H.B.K.	*Sanchez 9* (MO)
Tecomaria capensis (Thunb.) Spach	*Bayliss 1748* (MO)
Tourrettia lappacea (L'Her.) Willd.	*Davidse & Pohl 1689* (MO)
Tynanthus guatemalensis Donn. Sm.	*Gentry 7661* (MO)
Urbanolophium dusenianum (Kränzl.) Melch.	*Dusén 16997* (MO); *Reitz & Klein 4069* (US)
Xylophragma heterocalyx (Bur. & K. Schum.) A. Gentry	*Glaziou 14109* (P)
X. seemannianum (O. Ktze.) Sandw.	*Gentry 4975* (MO)

ADDITIONAL GENERIC MERGERS IN BIGNONIACEAE[1]

ALWYN H. GENTRY[2]

ABSTRACT

Five generic mergers in Bigoniaceae are proposed, largely as the result of palynological considerations. The proposed mergers are: *Orthotheca* with *Xylophragma*, *Neves-Armondia* with *Pithecoctenium*, *Paradolichandra* with *Parabignonia*, and both *Hanburyophyton* and *Pachyptera* with *Mansoa*. A new species, intermediate between *Mansoa* and *Pachyptera*, is described as *M. ventricosa* A. Gentry. New combinations required by the proposed mergers are: *Xylophragma heterocalyx* (Bur. & K. Schum.) A. Gentry, *Mansoa lanceolata* (DC.) A. Gentry, *M. alliacea* (Lam.) A. Gentry, *M. erythraea* (Dugand) A. Gentry, *M. hymenaea* (DC.) A. Gentry, *M. kerere* (Aubl.) A. Gentry, *M. kerere* var. *incarnata* (Aubl.) A. Gentry, *M. parvifolia* (A. Gentry) A. Gentry, *M. standleyi* (Steyerm.) A. Gentry, and *Parabignonia chodatii* (Hassler) A. Gentry. Transfer of *Neves-Armondia cordifolia* to *Pithecoctenium* necessitates a *nomen novum*, proposed as *P. hatschbachii* A. Gentry.

The palynological considerations summarized in the preceding paper suggest several additional taxonomic changes besides supporting various generic mergers previously proposed. It is the purpose of this paper to formally propose five generic mergers based in large part on this palynological evidence. These generic mergers include *Orthotheca* with *Xylophragma*, *Neves-Armondia* with *Pithecoctenium*, *Paradolichandra* with *Parabignonia*, and both *Hanburyophyton* and *Pachyptera* with *Mansoa*. The latter merger makes possible generic assignment of a problematical new species sharing features of *Pachyptera* and *Mansoa*.

ORTHOTHECA AND *XYLOPHRAGMA*

Xylophragma heterocalyx (Bur. & K. Schum.) A. Gentry, comb. nov.

Saldanhaea (?) *heterocalyx* Bur. & K. Schum. in Mart., Fl. Bras. 8(2): 254. 1897. TYPE: Brazil, Rio de Janeiro, *Glaziou 14109* (P, holotype; C, K, isotypes).
Orthotheca heterocalyx (Bur. & K. Schum.) Pichon, Bull. Soc. Bot. France 92: 226. 1945.

Orthotheca was proposed by Pichon (1945) as a monotypic segregate from *Saldanhaea* primarily because of its single 3-colpate pollen grains with finely granular exine. Unfortunately, Pichon failed to realize that this is exactly the type of pollen found in *Xylophragma*, with which *Orthotheca* agrees in other respects as well. Salient features include interpetiolar glandular fields, dendroid pubescence (in part), rather contracted axillary inflorescences, short, blunt pseudostipules, and puberulous corollas with rather pointed lobes. Taxonomic significance of the unusual frilly margined calyx which characterized this species is not clear, but in some flowers of the type collection the calyx apex has broken off calyptterately, and these differ hardly at all from those of *Xylophragma pratense* (Bur. & K. Shum. ex K. Schum.) Sprague and *X. myrianthum* (Cham.) Sprague.

As is the case with so many of the poorly known monotypic genera of Big-

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noniaceae which have been proposed, proper generic assignment makes specific, much less generic, recognition tenuous. The affinities of *X. heterocalyx*, a very rare species known only from the type collected in 1882, and a single recent collection [*Herringer & Azevedo 9885* (UB) from Minas Gerais, Brazil], are obviously with *Xylophragma pratense* of eastern Bolivia and adjacent Brazil, Peru, and Paraguay. While it is conceivable that it may one day prove to be an extreme of *X. pratense*, the unusual calyx seems adequate for specific recognition in the absence of either geographical or morphological intermediates, and a new combination is in order, though retention of *Orthotheca* is not.

Pachyptera, *Hanburyophyton*, and *Mansoa*

Mansoa DC., Rev. Bign. (Bibl. Univ. Genève) 12. 1838. LECTOTYPE: *M. hirsuta* DC.

Pachyptera DC. ex Meisn., Gen. 1: 299; 2: 207. 1840. LECTOTYPE: *P. foveolata* DC. = *M. kerere* (Aubl.) A. Gentry.

Adenocalymma sect. *Hanburyophyton* Bur. & K. Schum., Fl. Bras. 8(2): 87. 1896. LECTOTYPE: *A. splendens* Bur. & K. Schum. = *M. difficilis* (Cham.) Bur. & K. Schum.

Chodanthus Hassler, Bull. Herb. Boissier, sér. 2, 6: 151. 1906. TYPE: *C. splendens* (Bur. & K. Schum.) Hassler = *M. difficilis* (Cham.) Bur. & K. Schum.

Pseudocalymma Samp. & Kuhlm., O. Campo (Rio de Janeiro) 4(11): 15. 1933; Bol. Mus. Nac. Rio de Janeiro 10: 101. 1934. TYPE: *P. laevigatum* (Bur. & K. Schum.) Samp. & Kuhlm. = *M. hymenaea* (DC.) A. Gentry.

Onohualcoa Lundell, Contr. Univ. Michigan Herb. 7: 52. 1942. TYPE: *O. seleri* (Loes.) Lundell = *M. verrucifera* (Schlecht.) A. Gentry.

Bayonia Dugand, Caldasia 4:62. 1946. TYPE: *B. helicocalyx* (O. Ktze.) Dugand = *M. verrucifera* (Schlecht.) A. Gentry.

Hanburyophyton (Bur. & K. Schum.) Mello, Arq. Mus. Paranaense 9: 77. 1952.

Few better examples of the problems in generic delimitation which have plagued Bignoniaceae taxonomy exist than that of *Mansoa* and its relatives. The species of this complex are characterized by trifid tendrils, large lavender, purple, or white flowers, the corolla somewhat puberulous outside, at least on the lobes, an open, usually relatively few-flowered inflorescence, relatively (to *Arrabidaea*, etc.) wide linear-oblong fruit, and brownish seed wings hyaline only at the extreme ends. Other noteworthy features include the leaflets usually more or less 3-nerved basally, interpetiolar glandular fields usually present, petiolar glandular fields sometimes present, trifid tendrils, the branchlets subterete, more or less striate, often with a rather loose epidermis, and the vegetative parts often with a conspicuous onion or garlic odor. Members of this group have medium reticulate tricolpate or areolate pollen (see preceding paper).

De Candolle (1838, 1845) assigned most members of this group known by him to the two new genera *Pachyptera* and *Mansoa*, the former characterized by thick-winged (water-dispersed) seeds, the latter by its subulately toothed calyx. In their monumental *Flora Brasiliensis* treatment, Bureau & Schumann (1896–1897), adopting an over-broad concept of *Adenocalymma* as defined mainly by a relatively broad thick capsule, reduced *Pachyptera* to a section of *Adenocalymma*. Although *Mansoa* was theoretically recognized in the *Flora Brasiliensis*, two of the species treated under *Mansoa* were also redescribed with different names in *Adenocalymma* section *Hanburyophyton*. Later authors realized the important differences between the three sections attributed to *Adenocalymma* by

Bureau and Schumann and raised sections *Pachyptera* and *Hanburyophyton* to generic rank, the latter several times. As a result, the nine species of these two sections of the *Flora Brasiliensis* treatment, and several more recently described species related to them, have been apportioned subsequently to no less than nine genera (*Pseudocalymma, Pachyptera, Chodanthus, Hanburyophyton, Mansoa, Onohualcoa, Bayonia, Arrabidaea,* and one species retained in *Adenocalymma* sensu stricto) despite the fact that five of the nine were later considered to be conspecific! Unfortunately, the similarities among the species of these two groups and the similarity of both with *Mansoa* have not been sufficiently emphasized.

Sandwith (1947) remarked on the evident similarities of several of these genera, but actually united only *Bayonia* and *Onohualcoa*. Fabris (1965) merged *Chodanthus* with *Mansoa* on deciding that its type species, *C. praepensus* (Miers) Sandw. [a synonym is *C. splendens* (Bur. & K. Schum.) Hassler] was conspecific with *M. difficilis* (Cham.) Bur. & K. Schum. I have already united *Pseudocalymma* with *Pachyptera* (Gentry, 1973a) and *Onohualcoa* with *Mansoa* (Gentry, 1976). Additional evidence, especially from palynology, suggests the additional mergers of both *Hanburyophyton* and *Pachyptera* with *Mansoa*.

HANBURYOPHYTON

Bureau (1893) first used *Hanburyophyton* in his listing of Glaziou's collections as the generic name for the plant usually known as *Anemopaegma lanceolatum*. *Hanburyophyton* (with the single species *H. xanthinum* Bur.) was not formally described and must be treated as a nomen nudum. Bureau and Schumann (1896–1897) placed *Adenocalymma splendens* [now considered a synonym of *Mansoa difficilis*, see Sandwith (1954) and Fabris (1965)], along with several species later segregated as *Pseudocalymma* (see Gentry, 1973a) in section *Hanburyophyton* of *Adenocalymma*. This was the first valid publication of *Hanburyophyton*, but at the sectional level. Mello (1952) in his posthumously published notes on the Bignoniaceae of Brazil's Paraná State, took *Hanburyophyton* as the generic name for *A. splendens*, which he realized was distinct from *Adenocalymma*. Mello also correctly noted the affinity of his *Hanburyophyton* with *Mansoa*. No Latin description of *Hanburyophyton* was given, but Mello did refer to the *Flora Brasiliensis* treatment and *Hanburyophyton* (Bur. & K. Schum.) Mello appears to be a legitimate generic name. A type species has not been designated for *Hanburyophyton*, but the name has been applied only to *Anemopaegma lanceolatum* (as *H. xanthinum*) and that should be considered the type on historical grounds as well. However, *Anemopaegma lanceolatum*, though clearly distinct from *Anemopaegma*, proves referrable to *Mansoa*, and *Hanburyophyton* may be reduced to the synonymy of that genus.

Mansoa lanceolata (DC.) A. Gentry, comb. nov.

Tabebuia lanceolata DC., Prodr. 9: 213. 1845. LECTOTYPE: Brazil, Rio de Janeiro, *Guillemin 97* (P; MO, P, isolectotypes).

Bignonia xanthinum Mart. ex Bur., Vidensk. Meddel. Naturhist. Dansk Foren. Kjøbenhavn 1893: III. 1894., nom. nud. pro. syn.

Hanburyophyton xanthinum Bur., Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 1893: III. 1894, nom. nov. for *Tabebuia lanceolata* DC.

Anemopaegma lanceolatum (DC.) Bur. ex K. Schum., Nat. Pflanzenf. 4(3b): 215. 1894.

This misunderstood species was described by de Candolle (1845) citing collections of Lund and Guillemin from the vicinity of Rio de Janeiro. He described the corolla as white as noted by Guillemin. In 1893 Bureau placed *T. lanceolata* in the undiagnosed genus *Hanburyophyton* Bur. giving it the name H.(?) *xanthinum* Bur., based on Martius's earlier, but unpublished, *Bignonia* (*Alsocydia*) *xanthina*. Bureau cited *Glaziou 4713*, *4119*, *6647*, and *6814*, all from Rio de Janeiro, and doubtfully *Glaziou 4106* as belonging to the species.

There has been much taxonomic confusion of *H. xanthinum*, especially with *Mansoa difficilis*. Several additional collections at Paris have been determined as *H. xanthinum*, including *Glaziou 4109* which is sterile, but certainly a different species (simple tendrils, foliaceous pseudostipules, different leaf texture) probably belonging to *Anemopaegma* and *St. Hilaire s.n.* which is *Mansoa difficilis*. The specimens originally described as *Tabebuia lanceolata* were later transferred to *Anemopaegma* by Bureau (in herb.) and Schumann and most of them were treated as *A. lanceolatum* in the *Flora Brasiliensis*. However, one of the cited specimens (*Glaziou 4106*) was cited as *Adenocalymma splendens* (i.e., a synonym of *Mansoa difficilis*). There are two additional gatherings of this species in the Paris herbarium (*Miers 3080* and *Gardner 78/3*), both identified by Bureau as *Adenocalymma splendens*. (Two of the three sheets of *Miers 3080* at P have also been given different unpublished manuscript names under *Cydista* by Miers.)

The confusion of *Anemopaegma lanceolatum* with *Mansoa difficilis* is not surprising. This species proves to have the distinctive areolate pollen typical of *Mansoa* and is congeneric with *M. difficilis*. In fact, *M. lanceolata* is so close to *M. difficilis* that one might be tempted to treat the two as synonymous. However, the leaves of *M. lanceolata* can (usually) be distinguished from those of *M. difficilis* by their smaller size, more coriaceous texture, and more conspicuous reticulation. Its branches tend to dry darker and its calyx tends to be longer and more evenly truncate than in *M. difficilis*. The corolla is also more tubular with a relatively conspicuous, narrowly tubular basal portion; that of *M. difficilis* is more or less tubular-infundibuliform without a long and narrowly tubular basal portion.

The fruits of *M. lanceolata* have not been described, although one of the sheets of *Miers 3080* includes an immature fruit which is linear, 23 cm long, 9 cm wide, flat, drying black, scattered lepidote but otherwise glabrous, longitudinally striate-wrinkled, with the midline slightly raised. The fruit of *Hanburyophyton* is thus similar to that of *Mansoa* and utterly unlike the elliptic fruit of *Anemopaegma*, supporting its reduction to *Mansoa*.

The only anomalous characteristic is the yellow flower color (described as white by at least one collector) which I suspect is more cream than yellow and thus not completely out of place in an otherwise purple (or white)-flowered genus.

PACHYPTERA

As originally established by de Candolle, *Pachyptera* was primarily characterized by thick coriaceous seed wings. As orginally delimited, the genus was a hodgepodge of six species—the four for which flowering material was known are all synonymous with *Paragonia pyramidata* and another is referrable to *Macfadyena uncata* (Andr.) Sprague & Sandw. Only the type, now known as *P.*

kerere (Aubl.) Sandw., is referrable to *Pachyptera* as resurrected by Sprague & Sandwith (1932). Subsequently, I (Gentry, 1973a) have merged *Pseudocalymma,* characterized especially by its onion or garlic smell, with *Pachyptera,* while raising Dugand's *P. kerere* var. *erythraea* to species status and describing a rather anomalous microphyllous appressed-climbing species as *Pachyptera parvifolia*. Thus as currently constituted *Pachyptera* contains seven species, and is separated from *Mansoa* by the presence of interpetiolar (except *P. parvifolia*) and petiolar (usually) glandular fields, more evenly truncate calyces, a tendency to vertically seriate pseudostipules, ovules biseriate rather than ca. 4-seriate in each locule, frequent vegetative smell of garlic, and most important, tricolpate rather than areolate pollen grains.

New evidence has undermined most of these potential differentiating characters between *Pachyptera* and *Mansoa*. Merger of *Onohualcoa* with *Mansoa* includes species with the ovules biseriate in each locule in that genus. Several species of *Mansoa,* including its type, are now known to have an onion odor vegetatively. The new species described below is like *Pachyptera* in most features but has its subulate pseudostipules paired side by side rather than vertically seriate.

Only the palynological difference between 3-colpate *Pachyptera* and areolate *Mansoa* remains as a definitive separating character. However, the palynological survey reported in the preceding paper reveals that some species of *Pachyptera* actually have areolate pollen. This is true even within the group of three onion-smelling species formerly segregated as *Pseudocalymma,* which are so closely related that Sandwith (1954) considered them to be conspecific. *Pachyptera alliacea* has areolate pollen, *P. standleyi* has 3-colpate pollen, and *P. hymenaea* sensu lato may apparently have both pollen types plus an intermediate irregularly syncolpate form. Clearly pollen is too variable in this group to be a taxonomically reliable character for generic separation and the merger of *Pachyptera* with *Mansoa* seems in order.

The additional species of *Mansoa* are:

Mansoa alliacea (Lam.) A. Gentry, comb. nov.

Bignonia alliacea Lam., Encycl. 1: 421. 1785. TYPE: French Guiana, *Aublet s. n.* (P-AD).
Pseudocalymma alliaceum (Lam.) Sandw., Recueil Trav. Bot. Néerl. 34: 210. 1937.
P. alliaceum (Lam.) Sandw. var. *microcalyx* Sandw., Kew Bull. 1953: 467. 1954 (pro parte). TYPE: French Guiana, *Sagot 418* (K, holotype; BM, US, W, isotypes).
Pachyptera alliacea (Lam.) A. Gentry, Brittonia 25: 236. 1973.

Mansoa erythraea (Dugand) A. Gentry, comb. nov.

Pachyptera kerere var. *erythraea* Dugand, Caldasia 7: 16. 1955. TYPE: Colombia, Santander, *Romero-Castañeda 4727* (COL).
Pachyptera kerere (Dugand) A. Gentry, Phytologia 35: 186. 1977.

Mansoa hymenaea (DC.) A. Gentry, comb. nov.[3]

Bignonia hymenaea DC., Prodr. 9: 158. 1845. TYPE: Brazil, Bahia, *Blanchet 1434* (G-DC, holotype; P, isotype).

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[3] For complete synonymy (22 entries) see Gentry (1973b).

Pachyptera hymenaea (DC.) A. Gentry, Brittonia 25: 236. 1973.

Mansoa kerere (Aubl.) A. Gentry, comb. nov.

Bignonia kerere Aubl., Hist. Pl. Guiane Fr. 2: 644, *tab. 260*. 1775, non Lindl. TYPE: French Guiana, *Aublet s.n.* (BM, P-AD no. 12271, W).
Pachyptera kerere (Aubl.) Sandw., Recueil Trav. Bot. Néerl. 34: 219. 1937.

Mansoa kerere (Aubl.) A. Gentry var. *incarnata* (Aubl.) A. Gentry, comb. nov.

Bignonia incarnata Aubl., Hist. Pl. Guiane Fr. 2: 645, *tab. 261, 262, figs. 1–8*. 1775. TYPE: not seen.
Pachyptera kerere var. *incarnata* (Aubl.) A. Gentry, Brittonia 25: 235. 1973.

Mansoa parvifolia (A. Gentry) A. Gentry, comb. nov.

Pachyptera parvifolia A. Gentry, Phytologia 26: 448. 1973. TYPE: Colombia, Sur de Santandar, *Haught 2179* (MO).

Mansoa standleyi (Steyerm.) A. Gentry, comb. nov.

Pseudocalymma standleyi Steyerm., Publ. Field Mus. Nat. Hist., Bot. Ser. 23: 235. 1947. TYPE: Guatemala, Quetzaltenango, *Steyermark 33533* (F).
Pseudocalymma alliaceum var. *macrocalyx* Sandw., Kew Bull. 1953: 468. 1954. TYPE: British Guiana, Demerara River, *Jenman 6752* (K, holotype; NY, isotype).

Besides the above new combinations, an additional new species of *Mansoa*, referrable to the former *Pachyptera*, remains to be described:

Mansoa ventricosa A. Gentry, sp. nov.

Frutex scandens, ramuli teretes, consociebus glandularum in nodis inter petioles; pseudostipulae subulatae; folia bifoliata, interdum cirrho trifido, foliolis anguste ellipticis; inflorescentia floribus in panicula terminali dispositis; calyx cupulatus, minute 5-denticulatus, aliquantum lepidotus; corolla alba, ventricose infundibuliformi-campanulata super basem tubularem, extus puberula; stamina exserta, thecis parallelis; ovarium lineari-oblongum, ovulis in quoque loculo biseriatis; discus globosus; capsula ignota.

Liana; branchlets terete, minutely subpuberulous but ± glabrate, finely and evenly striate, drying brown, without noticeable lenticels; pseudostipules subulate, paired, ca. 3 mm long (cf. *Ceratophytum*); nodes with interpetiolar glandular fields. Leaves 2-foliolate, sometimes with a trifid tendril, elliptic or narrowly elliptic, acute to long-acuminate, cuneate to rounded at the base, 6–14 cm long, 1.8–7 cm wide, chartaceous, the main veins slightly raised below, glabrous above and below except for a few minute lepidote scales, drying olive above and below; petiolules 0.7–1.5 cm long, petiole 1.5–2.5 cm long, flattened above, glabrous or very slightly puberulous above. Inflorescence a terminal panicle with a well-developed central axis, somewhat puberulous and lepidote, the lower lateral branches with 2–3 flowers, the upper with 1; bracts and brateoles minute, scarcely evident; pedicels 1–2 cm long. Flowers with the calyx cupular, truncate, minutely 5-denticulate, 5–7 mm long, 5–7 mm wide, somewhat lepidote, very slightly puberulous, with irregular trichomes, the margin densely ciliate, with fields of plate-shaped glands near the margin; corolla white, conspicuously and ventricosely infundibuliform-campanulate above a 1.5 cm long tubular base, 4.3–5 cm long, 1.5–2 cm wide at the mouth of the tube, the tube 3–3.5 cm long, the lobes narrow,

1–1.5 cm long, the lobes puberulous outside, puberulous and glandular-lepidote inside, the tube outside densely puberulous above, glabrous on the narrowly tubular base, conspicuously glandular lepidote just above the base, the tube mostly glabrous within, villous with long trichomes at the base of the stamens; stamens didynamous, inserted 12–15 mm above the base of the corolla tube, the anthers exserted, the thecae parallel, 5–6 mm long, the pollen medium reticulate, 3-colpate, the longer filaments 3(+) cm long, the shorter filaments 2.7–2.9 cm long, the staminode 4 mm long; pistil ca. 5 cm long, the ovary linear-oblong, 4 mm long, 1 mm wide, subterete, densely puberulous, the ovules 2-seriate in each locule; disc spherical, contracted at the top into the base of the ovary, 2.5–3 mm in diameter. Fruit unknown.

TYPE: BRAZIL. PARA: Km. 345 along Belém-Brasilia highway, flowers white, 9 Aug. 1963, *B. Maguire, J. Murça-Pires, C. K. Maguire & N. T. Silva 56083* (MO, holotype; COL, NY, isotypes).

Additional collection examined: BRAZIL. MARANHÃO: 15 km s of Para-Maranhão border on Belém-Brasilia highway, liana, flowers white, in forest, 31 Aug. 1963, *Prance & Silva 58978* (UB).

Generic placement of this distinctive new species is somewhat problematical, expecially in the absence of fruit. Features such as trifid tendrils, striate branchlets, lack of petiolar glandular fields, and noticeably greater density of the corolla pubescence on the lobes in bud suggest *Mansoa* sensu stricto, which differs especially in lacking interpetiolar glandular fields and in having areolate pollen. *Pachyptera* shares most of those features as well as tricolpate pollen. The subulate pseudostipules are out of place in either *Pachyptera* or *Mansoa* and are remarkably like those of monotypic *Periarrabidaea*, which differs in light yellow tubular-infundibuliform corollas and pollen with a very finely reticulate almost psilate exine, but is vegetatively similar. Merger of *Pachyptera* and *Mansoa* makes generic assignment of intermediate *M. ventricosa* easier. However, its corolla shape is unlike any species of *Mansoa* or *Pachyptera* and is perhaps more like that of *Martinella*, a genus also similar in an unusual coarsely reticulate tricolpate pollen. The existence of this interesting intermediate species combining the features of so many genera would seem to undermine generic separation not only of *Pachyptera* and *Mansoa* but also of *Periarrabidaea* and perhaps even *Martinella* and *Leucocalanthe*.

NEVES-ARMONDIA AND *PITHECOCTENIUM*

Pithecoctenium hatschbachii A. Gentry, nom. nov.

Pithecoctenium cordifolium DC., Prodr. 9: 194. 1845, non Mart., Flora 24(2), Beibl. 48. 1841. TYPE: Brazil, São Paulo, *Martius 408* (M).

Neves-Armondia cordifolia K. Schum., Engl. & Prantl., Nat. Pflanzenf. Nachtrag 1: 302. 1897, based on *Pithecoctenium cordifolium* "Mart." (i.e. *P. cordifolium* DC.).

The single species of monotypic *Neves-Armondia* is so similar to *Pithecoctenium* that Martius (in herb.), followed by de Candolle (1845), identified his collection of *Neves-Armondia* with a plant from Cuyaba which he described as *P. cordifolium* but which is actually referrable to widespread *P. crucigerum* (L.) A. Gentry. In *Flora Brasiliensis*, Bureau & Schumann (1896–1897) noted the

glabrous ovary, unique in *Pithecoctenium*, of Martius's São Paulo collection and several other gatherings from coastal Brazil. Excluding the type from *P. cordifolium* Mart., they treated these under that name as a separate section *Leiogyne*. Subsequently, Schumann (1897) received a collection of the fruit of this species from Neves-Armond and was persuaded by its nonechinate surface to erect for the species a new genus, *Neves-Armondia*. The pollen of *Neves-Armondia* is exactly that of *Pithecoctenium*, as are the flowers (except the glabrous ovary) and all vegetative features. The vegetative characters (pellucid green-drying leaves) listed as diagnostic of section *Leiogyne* by Bureau and Schumann are actually shared with *P. crucigerum*, and *Neves-Armondia* cannot be distinguished from *P. crucigerum* in the absence of fruit without dissecting a flower to examine the ovary.

Since the epithet "cordifolium" is preempted in *Pithecoctenium*, return of this species to that genus necessitates a nomen novum. I have selected an epithet commemorating Gert Hatschbach, from whom I have received beautiful material of this rare plant and other Brazilian Bignoniaceae.

Paradolichandra and *Parabignonia*

Parabignonia chodatii (Hassler) A. Gentry, comb. nov.

Paradolichandra chodatii Hassler, Bull. Herb. Boissier, sér. 2, 7: 720. 1907. TYPE: Paraguay, Sierra de Amambay, *Hassler 10281* (*coll. Rojas*) (NY).

Monotypic, rarely collected *Paradolichandra* of Paraguay and adjacent parts of Brazil, Bolivia, and Argentina was described by Hassler (1907) in the absence of fruiting material as a new genus of Tecomeae because of its affinity with *Dolichandra*, which has fruits dehiscent perpendicular to the septum, but is anomalous in that tribe in being a tendrillate liana. *Paradolichandra* was also compared by Hassler with *Parabignonia*, the other tendrillate genus usually assigned to Tecomeae. Although *Paradolichandra* is adequately separated from *Dolichandra*, which differs especially in a spathaceous calyx, stipitate ovary and fruit, tubular strongly bilabiate corolla, and exserted anthers with parallel thecae, its separation from poorly known *Parabignonia* is more tenuous. The differentiating characters listed by Hassler are: lepidote calyx, sessile ovary, ovules multiseriate in each locule, and a paniculate inflorescence. Hassler provided a key to these genera, all monotypic, (also to the illegitimate *Odontotecoma* which Sandwith (1959) demonstrated to have been based on a mixed collection) which emphasized the additional character of a double disc in *Paradolichandra* versus a simple disc in *Parabignonia*.

Fabris (1965, Meyer & Fabris, 1953) reported *Paradolichandra* from the Yungas region of northwest Argentina and described its fruit for the first time. The fruit of *Paradolichandra* proved to be linear and loculicidal, exactly like that of *Parabignonia*. Despite his description of its fruit as loculicidal, Fabris placed *Parabignonia* with Bignonieae in his treatment of Bignoniaceae for *Flora Argentina*, although he retained *Dolichandra* itself in Tecomeae. The "double" disc of *Paradolichandra* as figured by Fabris is actually conical with an indistinct groove separating its apical and basal portions.

Sandwith (1966) described a second species of *Parabignonia* and discussed

the relationships of *Paradolichandra*, *Dolichandra*, and *Parabignonia*. Retaining them in Tecomeae, he noted the close relationship of the three genera and suggested that *Paradolichandra* might have to be reduced to *Parabignonia*. As summarized by Sandwith, the only differences between *Paradolichandra* and *Parabignonia* are the former's densely lepidote calyx, glabrous outer surface of the corolla, and double disc. Sandwith also emphasized that *Parabignonia* and *Dolichandra* had been described by Urban (1916) and Gomes (1955) as having pollen with a distinctly granular or microreticulate exine while *Paradolichandra* was variously described as having either a smooth or a reticulate exine.

It seems evident that these characters are inadequate for generic differentiation, especially as they are all a matter of degree. The calyx of *Parabignonia steyermarkii* Sandw. is also somewhat lepidote. One species of *Parabignonia* has the corolla tube puberulous outside, while the other has the tube glabrous, just as in *Paradolichandra*, though the lobes are puberulous. The disc of *Parabignonia* also has a tendency toward a basal annulus. Both genera have sessile ovaries with the ovules irregularly 3–5-seriate in each locule. The pollen of both *Paradolichandra* and *Parabignonia* proves to be similarly tricolpate and psilate-foveolate (see above), clinching the argument for their merger.

Tribal reassignment of *Dolichandra* and *Parabignonia* is also supported by the palynological evidence. The almost psilate pollen of *Dolichandra* and *Parabignonia* would ally them in Bignonieae with *Macfadyena* and *Melloa*, which have similar large calyces, trifid more or less uncate tendrils, and multiple phloem arms in stem cross-section. Although *Macfadyena* has fruit dehiscence parallel to the septum, *Melloa* has apparently 4-valved fruits with each valve splitting in half and is thus dehiscent both parallel to and perpendicular to the septum. *Parabignonia* was described as having dehiscence perpendicular to the septum, but only two immature fruits of the genus have been available for study, the collection on which Bureau & Schumman's (1896–1897) description was based apparently having been destroyed in Berlin. Recently I received from G. Hatschbach a beautiful fruiting collection of *Parabignonia unguiculata* (Vell.) A. Gentry (*Hatschbach 39143*, Porto Barreiro, Paraná, Brazil). The mature fruit is clearly "4-valved," dehiscent both parallel to and perpendicular to the septum as in *Melloa*. Moreover, the capsule valves of both *Macfadyena* and *Dolichandra* are occasionally centrally split [e.g., *Croat 9151* (MO) for *Macfadyena*; *Pederson 4541* (MO) for *Dolichandra*], strongly suggesting that direction of fruit dehiscence in this group does not have the same taxonomic significance as elsewhere in the family. Despite their differences in fruit dehiscence, these genera form a natural group.

On the other hand, the almost psilate pollen of *Dolichandra* and *Parabignonia* would ally them in Tecomeae only with *Jacaranda* and *Digomphia*, genera which are utterly different in every other respect. That the palynological evidence suggests affinities with a morphologically similar group in Bignonieae but not in Tecomeae provides additional evidence in favor of their tribal transfer to Bignonieae.

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STRUCTURAL, BEHAVIORAL, AND PHYSIOLOGICAL ADAPTATIONS OF BEES (APOIDEA) FOR COLLECTING POLLEN[1]

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ABSTRACT

Bees, like their wasp relatives, forage for and transport food to a nest as provisions for their offspring. Unlike female Sphecoidea which transport arthropods one at a time as prey, bees transport pollen requiring specialized scopal (brush) or corbicular (fringed plate) structures to transport the dustlike material externally. Scopae often exhibit further modifications in density and amount of plumosity in relation to the size and ornamentation of the pollen grains they transport. Bees also differ from sphecid wasps by possessing branched body hairs that are relatively densely packed. These hairs, the electrostatic surface potential, and specialized hair groups for extraction of hidden pollen are important in the acquisition of pollen from flowers. Structures for grooming (brushes, combs, and scrapers) and grooming behavior patterns are modified to permit manipulation and packing of pollen in the specialized transport structures. The addition of nectar, so that pollen is packed moist, is a behavior that permits the carrying of pollen of a great variety of sizes and ornamentations in relatively simplified scopae or in corbiculae. The addition of oils to the diet of some bees has resulted in a modified type of scopal structure that has a wooly area basally and stiff guard hairs extending distally and that can transport a mixture of oil and pollen. Special hairs on the fore and mid basitarsi and teeth of hind tibial spurs are modified as oil scraper and manipulation structures. The use of corbiculae in Apidae to transport nesting materials and the hind tibiae in male orchid bees (Euglossini: Apidae) for transporting aromatic compounds involves behavior patterns similar to those for pollen transport in grooming, manipulating, and packing the materials. Other behavioral and physiological adaptations important in the location and acquisition of pollen by bees include individual constancy, oligolecty, seasonal synchrony, preimaginal conditioning, daily synchrony, buzz pollination, and other responses to specific modes of pollen presentation. Most of the behavioral patterns involve learning. They may be modified by extrinsic factors, and they may modify intrinsic structural and physiological characters.

Bees share a common ancestry with sphecoid wasps, but feed on plant materials rather than arthropod prey. Like their wasp relatives, female bees forage from a nest to which they must transport food for their offspring. Sphecoid wasps commonly transport single arthropods held in the mandibles often assisted by the legs, but some advanced sphecids transport their prey in a more rearward position supported primarily by the mid legs or occasionally by special modifications of the sting or pygidial plate (Evans, 1962). Since pollen, the principal brood food of Apoidea, occurs primarily as a fine-grained (5–210 μm), dustlike material, most bees have evolved highly specialized adaptations for pollen transport. Most bees carry some pollen mixed with nectar in the crop or honey stomach. Few bees transport pollen exclusively in the crop as do honey wasps (*Pseudomasaris*: Masaridae) (Torchio, 1970). However, females of all other nonparasitic bees transport pollen externally in specialized structures called scopae (brushes of hairs)

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or corbiculae (flattened or concave plates with long curved hairs on one or more sides). These unique structures are often further modified in relation to specific types of pollen carried. Structures and behavior for grooming are also modified for manipulation and packing pollen. Other behavioral and physiological adaptations are important, the location, synchronization, and host specificity of bees with their pollen plants. Many of these topics have been studied independently, but this paper attempts to present a broad overview for integration of the diverse adaptations of bees for acquiring, manipulating, and transporting pollen, based largely on my own observations and the literature on North American bees.

Structures for Pollen Transport

Phylogenetic trends appear in a distal shift in position of the scopal region of the hind legs (Pasteels & Pasteels, 1979) and restriction of the body surface used for pollen transport in bees (Table 1). The primitive scopa in female bees that transport pollen dry includes the trochanter through the tibia of the hind leg (Fig. 1) with accessory scopal areas of different relative importance in various tribes including hairs on the anterior abdominal sternites, hind coxa, hind basitarsus, and laterally on the propodeum and anterior abdominal tergites. The propodeal and femoral areas are sometimes bare centrally and referred to as corbiculae. These are found in the Colletidae, Oxaeidae, Andrenidae, and Halictidae (e.g., Pasteels & Pasteels, 1976, 1979; Roberts & Vallespir, 1978). Simple scopal hairs restricted to the abdominal sternites are characteristic of female pollen collecting Megachilidae (Pasteels & Pasteels, 1974). The Fideliidae carry pollen in the same manner and position as the Megachilidae (Rozen, 1970, 1973, 1977), and the hairs comprising the abdominal scopa appear essentially the same under the scanning electron microscope (Pasteels & Pasteels, 1975). The modified hind legs of Fidelliidae females do not transport pollen as suggested by earlier authors, but are used to flip sand from the nest entrances during excavation (Rozen, 1970, 1977). Females of Melittidae and nonparasitic Anthophoridae have scopal hairs restricted primarily to the hind tibia and basitarsus. The most specialized pollen transport structures are the corbiculae of the hind tibia in female pollen-collecting Apidae (Michener et al., 1978).

Exceptions to these trends in position occur when female bees mix pollen and nectar. Female Hylaeinae and Euryglossinae (Colletidae) transport pollen mixed with nectar in the crop or honey stomach (Jander, 1976; Roberts & Vallespir, 1978), and there is no evidence of an external transport apparatus (Pasteels & Pasteels, 1976). Although some authors suggest pollen is transported in the same manner by the Xeromelissinae (=Chilicolinae), Eickwort (1967) describes the scopa of a *Chilicola* as consisting of hairs on metasomal sternites 1–3, the femur of the hind leg, and as accessary scopae, hairs on the hind tibia, trochanter, and coxa, while Toro & Michener (1975) describe another *Chilicola* with scopal hairs on the hind femur and metasomal sternites 2–3. The discrepancies may be due to variability among species since neither Michener (1944) nor Pasteels & Pasteels (1976) found evidence of external scopae on the species they examined. Restriction of the scopal area in female Panurginae (Andrenidae), except *Panurgus*, is related to their behavior of adding nectar to the pollen as it is packed around the hind tibia. The corbiculae of Apidae (Fig. 6) transport pollen mixed with nectar

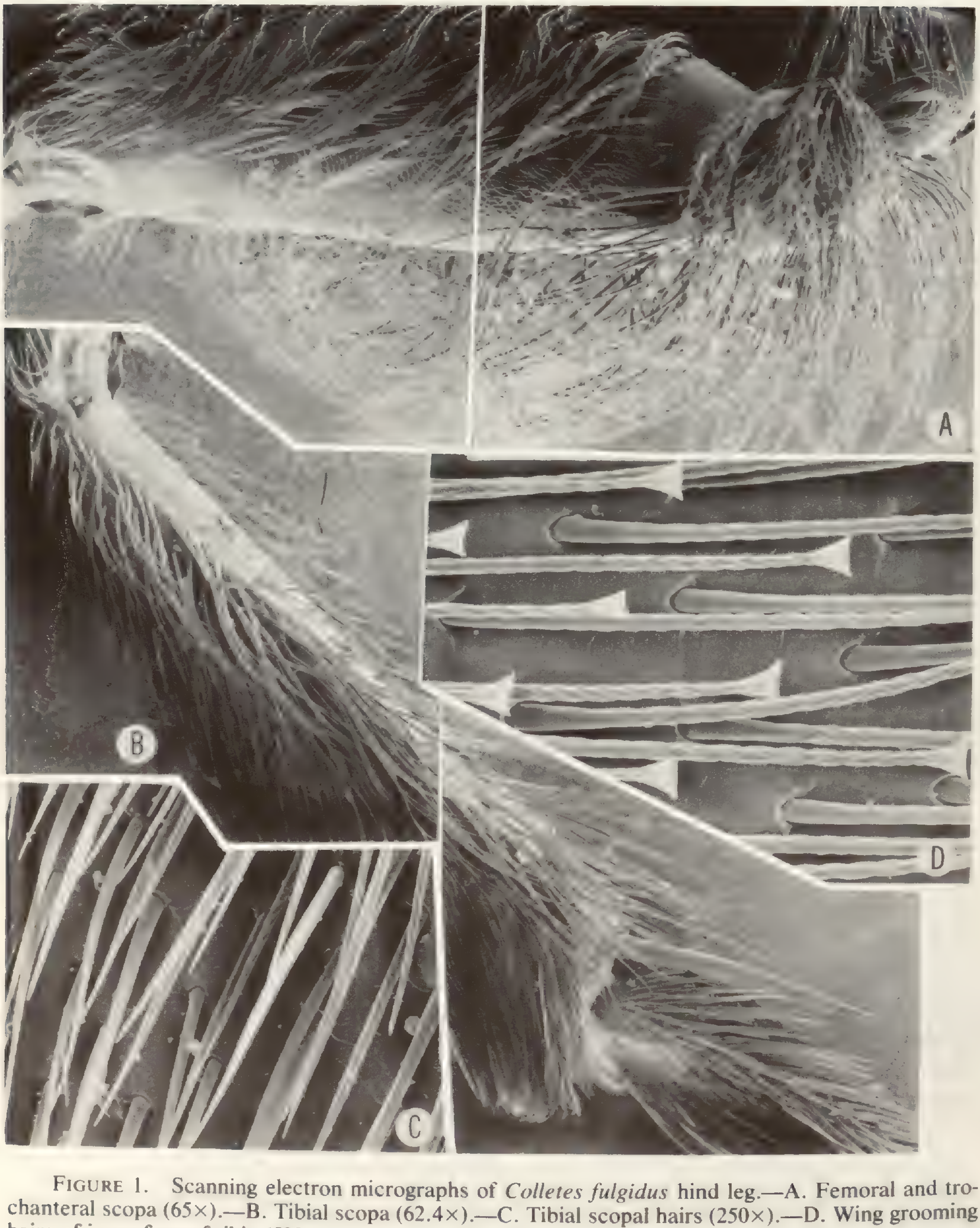


FIGURE 1. Scanning electron micrographs of *Colletes fulgidus* hind leg.—A. Femoral and trochanteral scopa (65×).—B. Tibial scopa (62.4×).—C. Tibial scopal hairs (250×).—D. Wing grooming hairs of inner face of tibia (500×).

or honey in the form of doughlike pellets. The eusocial *Lestrimelitta* (Meliponinae: Apidae) obtain pollen by robbing nests of other social Apidae. Since their workers have no corbiculae as do other Apidae, pollen is transported in the crop mixed with honey (Michener, 1974). Female Anthophoridae and Melittidae that transport pollen moistened with oil do not have more restricted scopal areas than their relatives that transport pollen dry (Roberts & Vallespir, 1978). The same is true of Melittidae that moisten their pollen loads with nectar.

TABLE 1. Location of pollen transport structures in Apoidea. The number of + indicates relative importance, the ± indicates deviation from subfamily mode. (Modified after Roberts & Vallespir, 1978.)

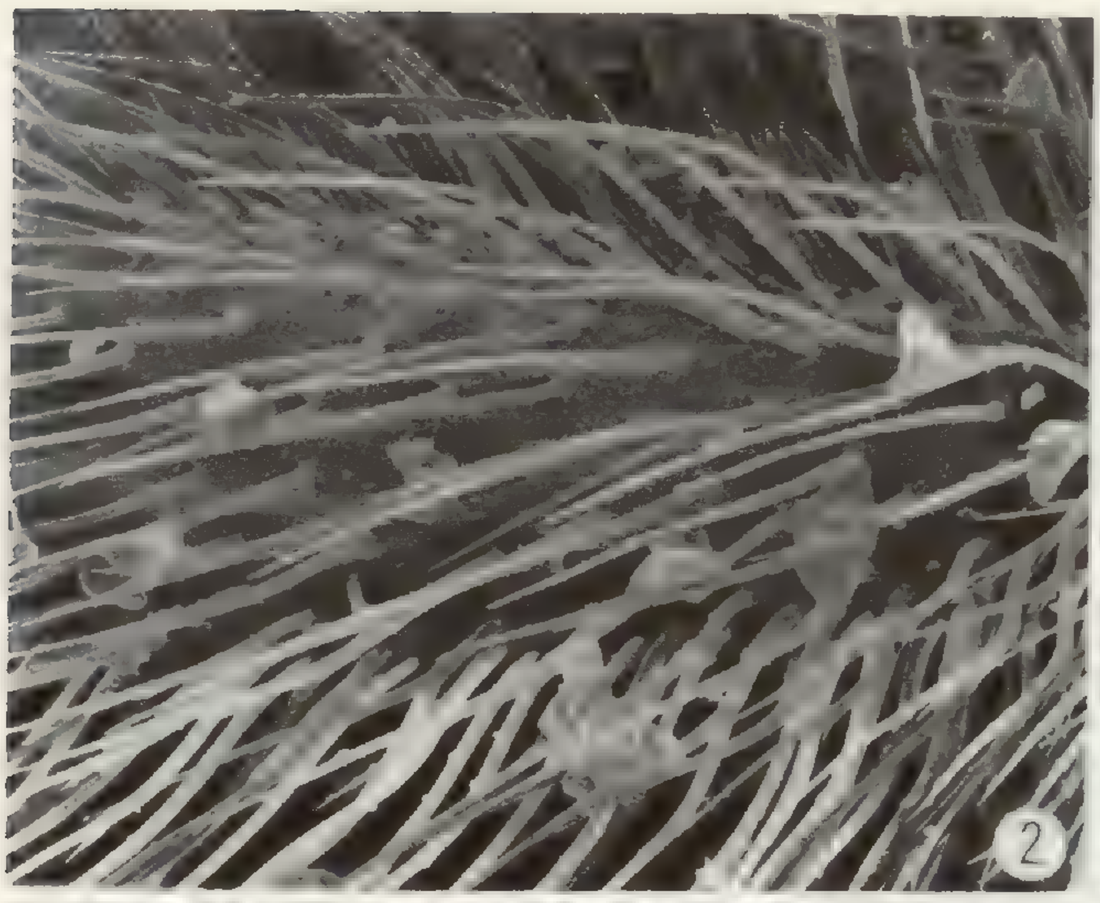
	Location							
			Hind Leg					
FAMILY Subfamily	Crop	Propo-deum	Coxa	Tro-chanter	Femur	Tibia	Basi-tarsus	Meta-somal[e] Sterna
COLLETIDAE								
Colletinae		++		++	+++	+++		
Diphaglossinae[a]		++		++	+++	+++		+(1–5)
Xeromelissinae			+	+	++	+		+++(1–3)
Hyaelinae	+++							
Euryglossinae	+++							
Stenotritinae				+	+++	+++	+	
OXAEIDAE[a]		++		++	+++	+++		+(1–2)
ANDRENIDAE								
Andreninae		++		++	+++	+++		
Panurginae						+++	±[e]	
HALICTIDAE								
Halictinae		+		+	+++	+++	+	+(1–5)
Nomiinae		+		+	+++	+++	+	+(1–5)
Dufoureinae		+		+	+++	+++	+	+(1–3)
MELITTIDAE								
Melittinae						+++	+++	
Dasypodinae						+++	+++	+(2–6)
Macropidinae						+++	+++	
Ctenoplectrinae						+++	+++	
FIDELIIDAE								+++(2–6)
MEGACHILIDAE								
Lithurginae								+++(2–6)
Megachilinae								+++(2–6)
ANTHOPHORIDAE								
Nomadinae[b]								
Anthophorinae			+[d]			+++	+++	+[d](2–5)
Xylocopinae						+++	+++	
APIDAE								
Meliponinae						+++		
Bombinae						+++		
Apinae	±[c]					+++		

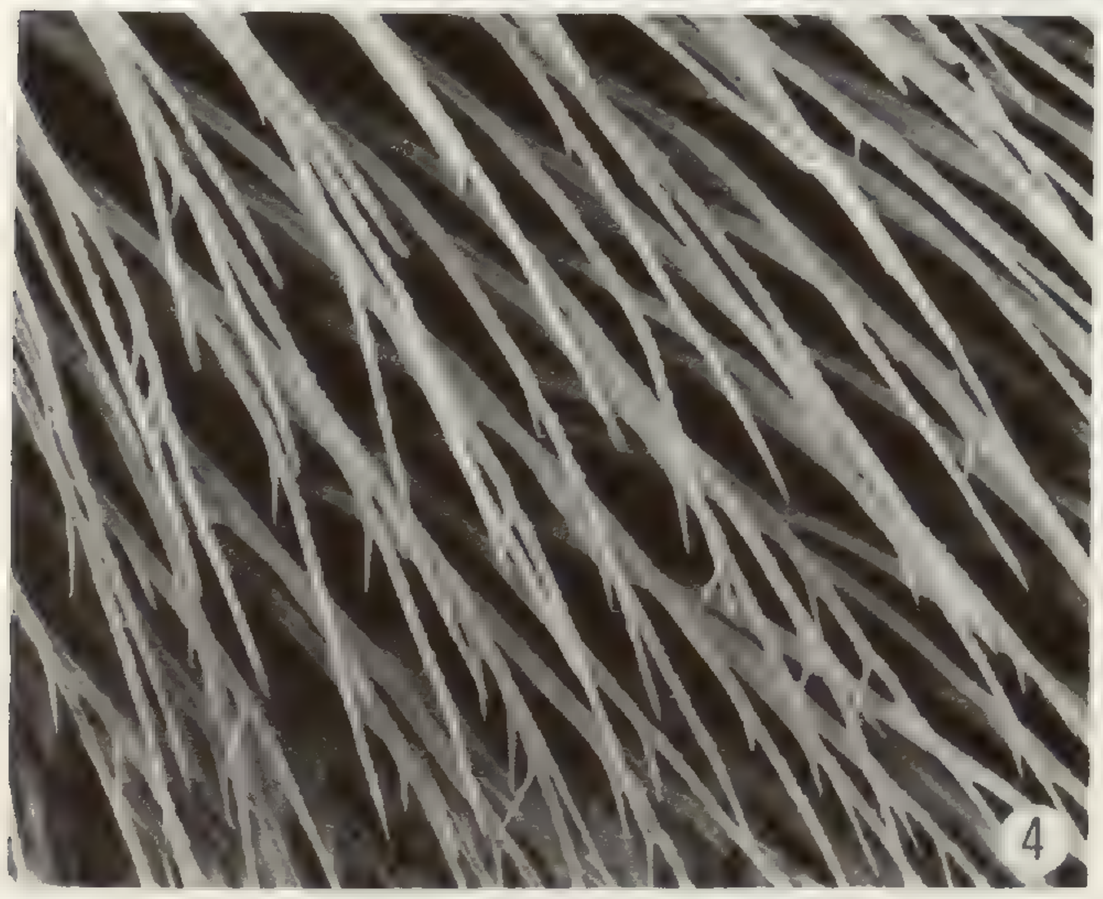
[a] Also laterally on metasomal tergite 1.
[b] All cuckoo bees, none transport pollen.
[c] Only robber bees, *Lestrimelitta*, that lack corbiculae.
[d] Some Eucerini (e.g., *Svastra*).
[e] Only *Panurgus* females that carry pollen dry on tibia and basitarsus.
[f] Metasoma = apparent abdomen (Michener, 1944, 1974). Numbers (in parens) = metasomal segments bearing scopal hairs. The more familiar term, abdomen, is used in the text, except for reference to specific segments.

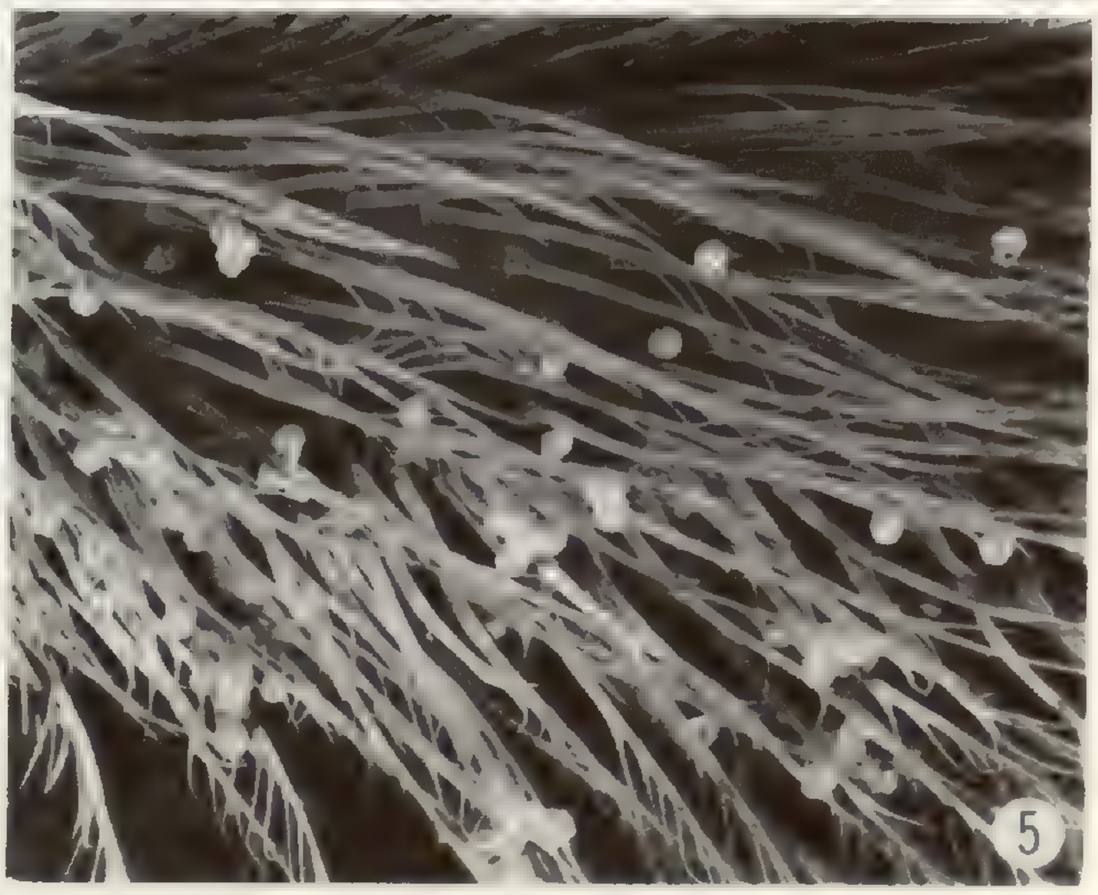
Further modifications of scopae involve deviations from near relatives based on spacing, length, and plumosity of the scopal hairs. Adaptations of these characters occur especially in host specific bees in relation to the size and ornamentation of the pollen grains they collect. Bees that collect small (<40 μm) pollen grains and transport them dry such as Oxaeidae and Caupolicanini (Diphaglossinae: Colletidae) (Linsley & Cazier, 1963) often have very densely packed and multibranched scopal hairs (Pasteels & Pasteels, 1976; Roberts & Vallespir, 1978). Bees that specialize on large (>100 μm) pollen grains such as *Xenoglossa* (Anthophoridae) on *Cucurbita* (Cucurbitaceae) (Hurd & Linsley, 1967) often have scopal hairs which differ from those of their relatives in being stouter and unbranched (Roberts & Vallespir, 1978).

The scopal hairs of most oligolectic (pollen specialist) bees that collect pollen from the Onagraceae tend to be long and simple in contrast to those of their relatives (Linsley, 1958; Thorp, 1969; Pasteels & Pasteels, 1979). This is due to the large size of the pollen grains and to the presence of viscin threads (Skvarla et al., 1978) that tie the grains into webby masses which can be packed only with difficulty in scopae with closely spaced, branched hairs or the corbiculae of *Apis* (Linsley et al., 1963a). All 24 species of *Andrena* (*Onagrandrena*) are oligolectic on Onagraceae and have sparse scopae composed of unbranched setae (Linsley et al., 1963a, 1963b, 1964, 1973; MacSwain et al., 1973). Ten of the 25 species of the related *Andrena* (*Diandrena*) share the same oligolectic behavior and scopal adaptation to Onagraceae (Figs. 2–3), while most other *Diandrena* are oligoleges on Compositae and have dense scopae with branched hairs (Figs. 4–5) (Thorp, 1969). *Lasioglossum* (*Evylaeus*) *oenotherae* Stevens and *L.* (*Sphecodogastra*) *texanus* Cresson have similarly simplified wide set scopal hairs contrasting sharply with the denser scopae of plumose hairs of other *L.* (*Evylaeus*) species as shown in the SEM photos by Pasteels & Pasteels (1979). The scopae of *Melissodes* (*Callimelissodes*) *clarkiae* LaBerge and *Diadasia angusticeps* Timberlake, although containing branched hairs, are modified to handle *Clarkia* pollen in contrast to their closest relatives (MacSwain et al., 1973). The *Melissodes* has scopal hairs with fewer long slender branches than do other members of the genus (LaBerge, 1961). The scopal hairs of *D. angusticeps* are more separated and do not completely conceal the hind tibial surface, as they do in other *Diadasia* examined, which appear more closely packed and conceal the tibia. Several other oligoleges of Onagraceae do not show special modifications since their closest relatives possess simple scopal hairs (e.g., *Megachile, Synhalonia,* and *Anthophora*); have reduced scopae (e.g., *Ceratina*); or pack their pollen moist in loose scopae (e.g., *Perdita* and *Hesperapis*) and are thus preadapted to handle onagraceous pollen.

The hind tibial corbicula of *Apis* (Fig. 6) and its accessory structures (Figs. 7–8) have been well described and figured by Casteel (1912) and Hodges (1952). The important elements are the slightly concave outer face of the apically widened tibia which is surrounded by long curved simple hairs (Fig. 6). Near the apicoposterior corner is a single long hair and between it and the apical margin is a row of minute apically flattened hairs (Fig. 7). At the base of the hind basitarsus, opposite these hairs is a plate that is angled toward the outer face of the tibia and is covered with small tubercles, the auricle (Fig. 7). On the inner face of the hind





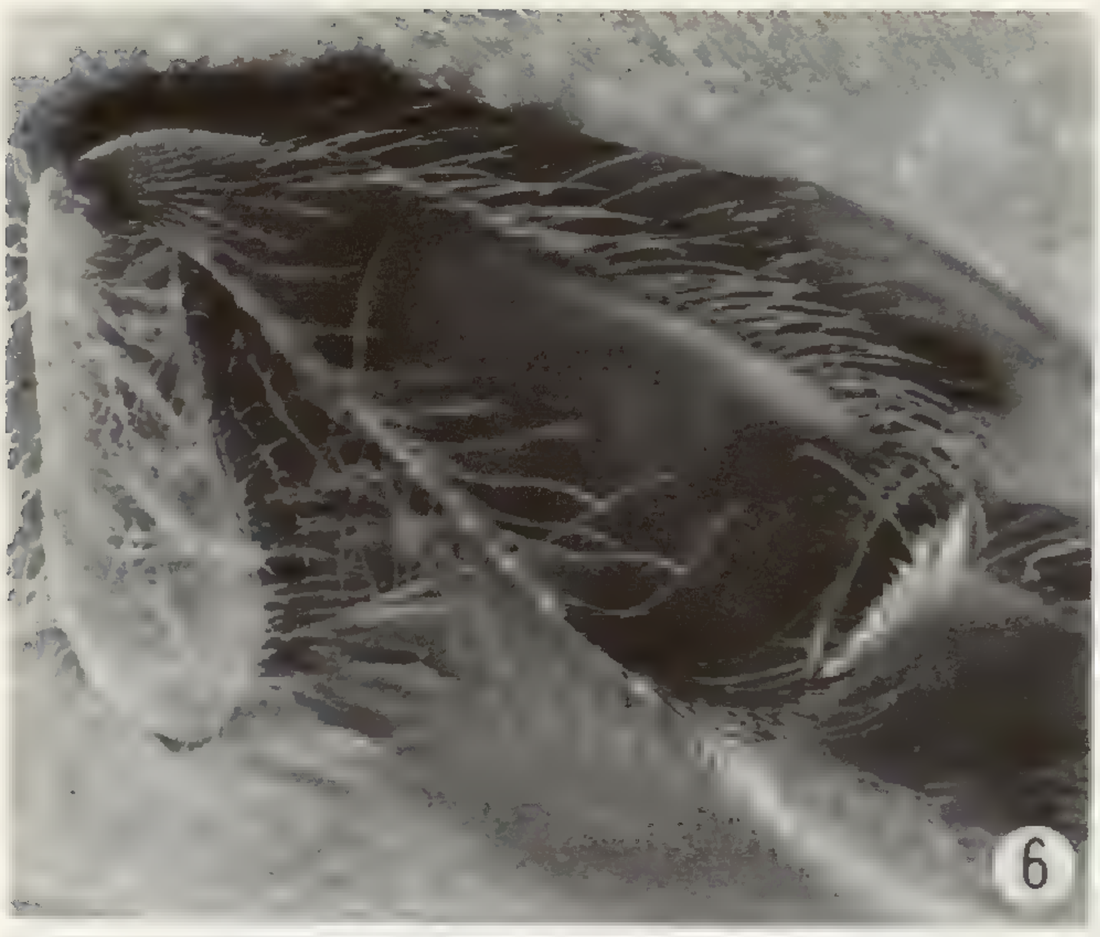


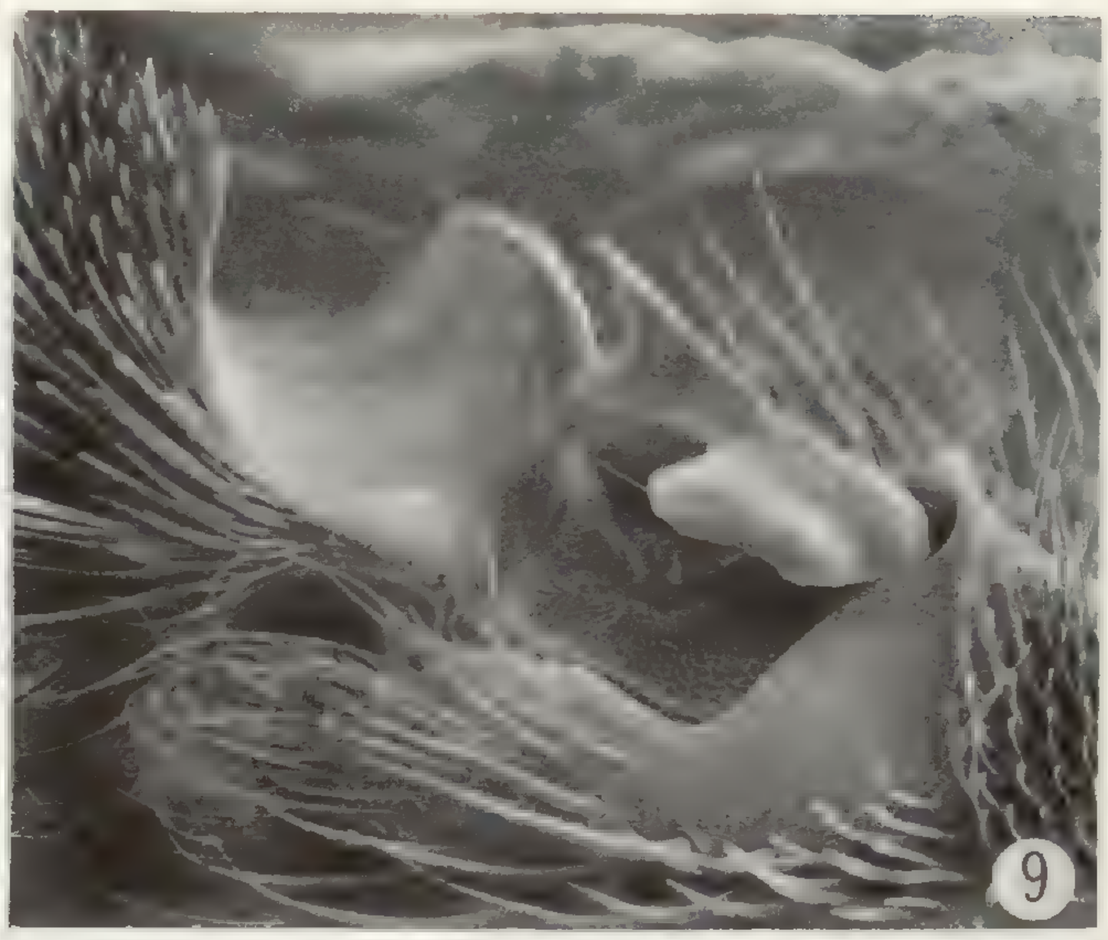
FIGURES 2–5. SEM of *Andrena* (*Diandrena*) hind tibial scopae.—2–3. Simple hairs of *Camissonia* (Onagraceae) oligoleges.—2. *A.* (*D. sperryi*) (100×).—3. *A.* (*D.*) *macswaini* (50×).—4–5. Branched hairs of oligoleges on Compositae.—4. *A.* (*D.*) *submoesta* on *Lasthenia* (200×).—5. *A.* (*D.*) *chalybioides* on *Agoseris* (80×).

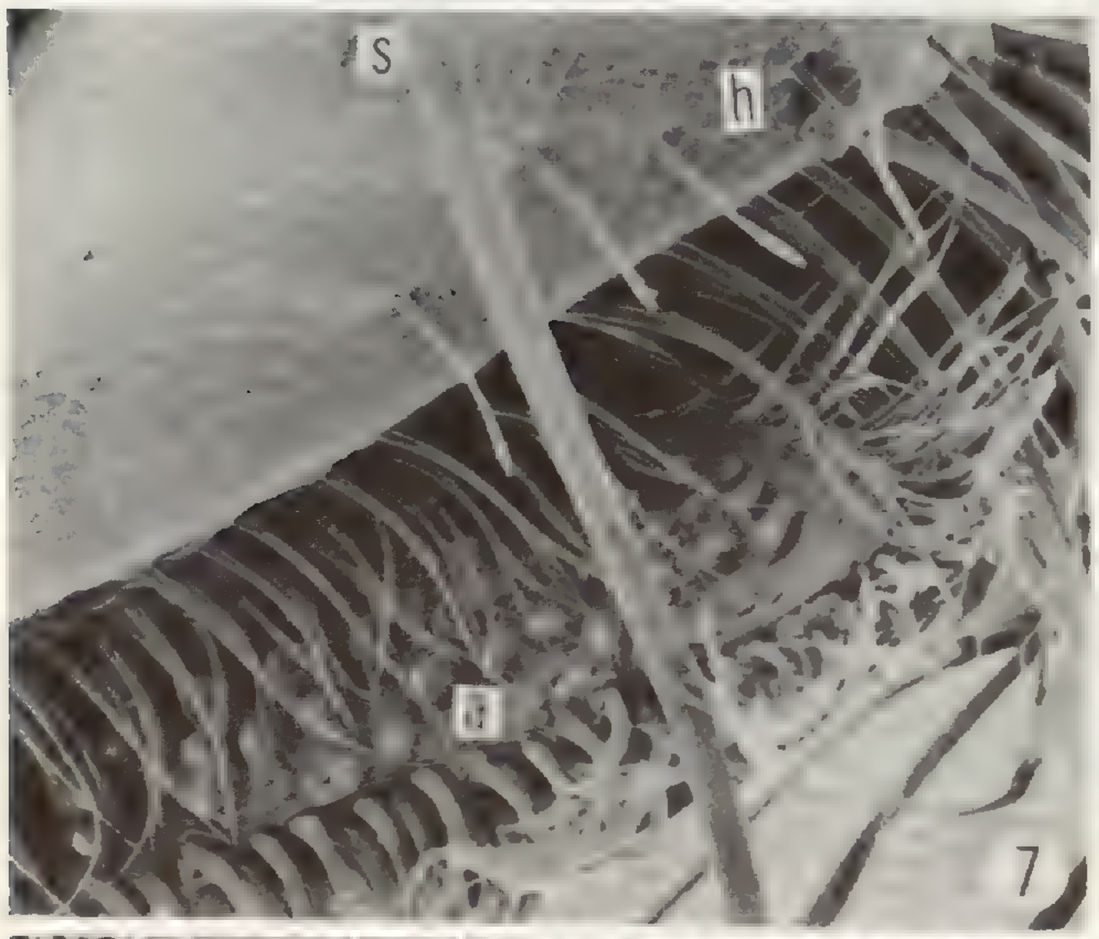
tibia is a comb of stout setae, the rastellum (Fig. 8). The corbicular structures of *Bombus* are similar, the hind tibial apex of Euglossini is very expanded and the auricular area and rastellum are relatively small, and the Meliponinae lack the auricle and often have a stiff elongate hair comb projecting posteriorly from the anteroapical corner of the hind tibia, the pencillum (Winston & Michener, 1977; Michener et al., 1978).

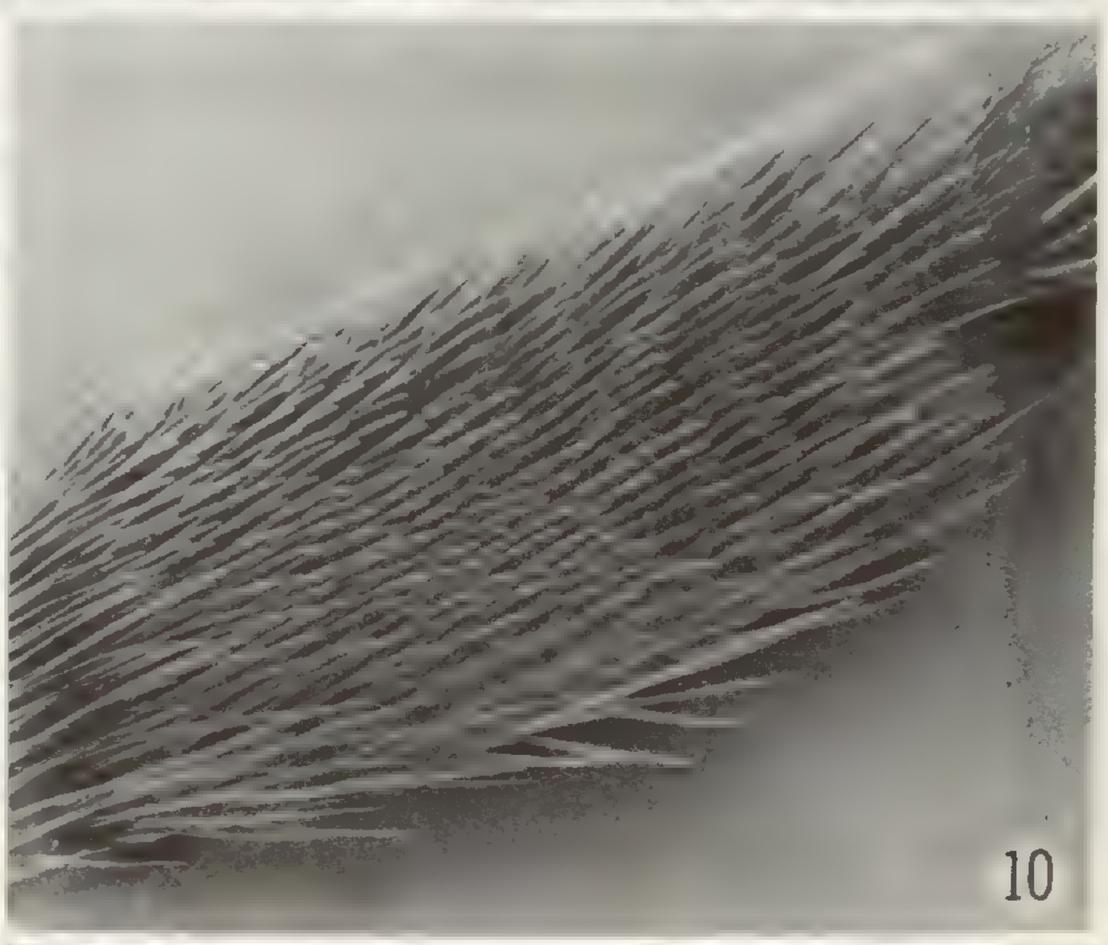
POLLEN MOISTENING BEHAVIOR

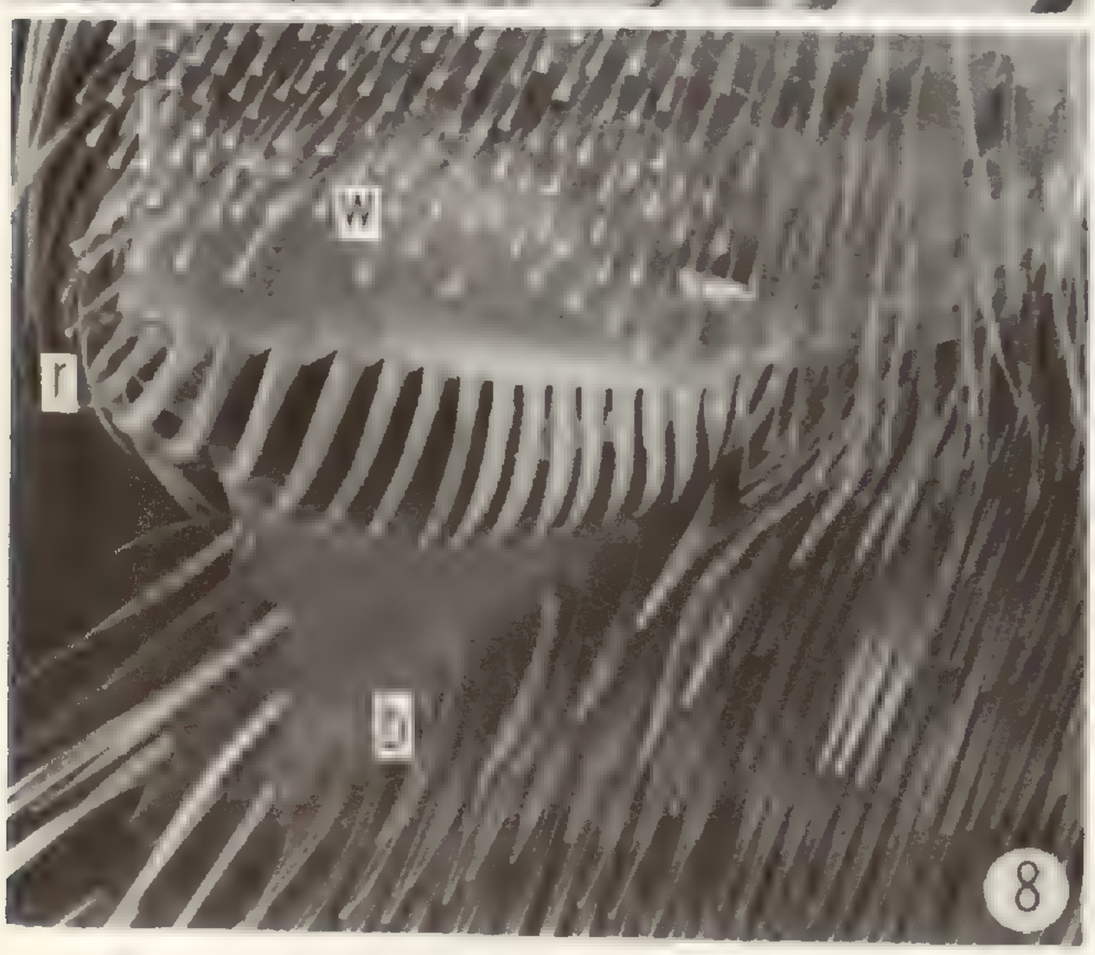
The behavior of moistening pollen by adding nectar or oil to it as it is packed in an external transport apparatus allows a wide variety of pollen grains with different sizes and surface ornamentations to be transported by the same apparatus. Thus, the scopae of female Panurginae (Andrenidae) and Melittidae that add nectar to their pollen loads consist of sparse, short, only moderately branched hairs. Females of these groups may be oligolectic on flowers with extremely small pollen (e.g., Boraginaceae), large pollen (e.g., Cactaceae, Malvaceae), or large pollen with viscin threads forming webby masses (e.g., Onagraceae). Pollen is also packed moist with nectar or honey in the types of corbiculae of the Apidae.











FIGURES 6–11. SEM of *Apis mellifera* corbicula, accessory pollen packing and grooming structures.—6. Corbicula of hind leg (20×).—7. Tuberculate surface of auricle of base of hind basitarsus (a) with single hair (s) and row of minute flattened tip hairs (h) of tibial corbicula above (270×).—8. Inner face of hind tibiobasitarsal junction with rastellum (r), wing grooming hairs (w), and basitarsal brush (b) (65×).—9. Antennal cleaner of fore leg with apically expanded brush hairs of the inner face of the basitarsus and adjacent tibial field (80×).—10. Brush of trochanteral venter and adjacent field at base of femur of mid leg (55.2×).—11. Brush of inner face of mid basitarsus (42×).

This permits considerable flexibility with host specialization at the individual level, but generalization at the population or species level. This flexibility is important in a group of predominantly social species whose colonies survive beyond the bloom period of their floral hosts.

The scopae of bees that add oil to their pollen loads may consist of two types of hairs: long, stiff, unbranched guard hairs and short, flexible, multibranched hairs forming a woolly underlayer (Linsley & Cazier, 1963) (Fig. 12); or of one type that has a long, stiff shaft with dense, short, slender branches basally but not apically. Functionally, the two types are similar with the oil being trapped in the dense undercoat, while the stiff guard hairs provide protection and support (Roberts & Vallespir, 1978).

Structures for Acquiring Pollen

The relatively dense vestiture of bees often with long hairs that branch (cf. Pasteels & Pasteels, 1972) in contrast to the sparse, short simple hairs of sphecoid wasps, provides a large surface for pollen acquisition. The electrostatic charges on the surface of bees are influenced by environmental conditions and may cause effects in bee behavior (Erickson, 1975; Warnke, 1976). Bees returning to a hive have positive surface potentials that tend to be higher than those leaving, indicating flight activity increases charge (Erickson, 1975). Since a high percentage of pollen carries a negative electrostatic charge (Stanley & Linskens, 1974), the differences in electric potential may enhance accumulation of pollen on the surfaces of bees.

Accessory structures for extracting pollen from certain flowers have evolved on some female bees. These involve specialized long hairs, usually hooked or wavy at the tips, near the mouthparts, or on the proboscis, (Figs. 14–15) or fore legs (Michener, 1944; Timberlake, 1954; Stage, 1966; Zavortink, 1972) (Table 2). Similarly, most female anthophorid bees that collect and add oils to their pollen loads have special combs on the fore and mid basitarsi (Fig. 13) for manipulating the oil (Vogel, 1974; Simpson et al., 1977; Roberts & Vallespir, 1978). Hind tibial spurs of bees that transport oils are often conspicuously pectinate (Roberts & Vallespir, 1978).

Structures for Grooming and Pollen Manipulation

In addition to morphological adaptations for extracting and transporting pollen, structures involved in normal grooming behavior have been elaborated and new structures evolved for manipulation and transfer of pollen from the body surface of bees into their transport structures (Table 3). The concept of morphogenetic fields of hair types on bees was proposed by Pasteels & Pasteels (1973). It is supported by their subsequent studies with the scanning electron microscope on the structure, function, location, and evolution of hair types in bee scopae (Pasteels & Pasteels, 1974, 1975, 1976, 1979). These authors find that where fields of different hair types are contiguous the boundary contains hairs tending to be morphologically intermediate or an irregular mosaic of several hair types. These authors also have identified "regional fields" in which a hair type occurs on adjacent segments and may grade into other hair types peripherally. Abdominal

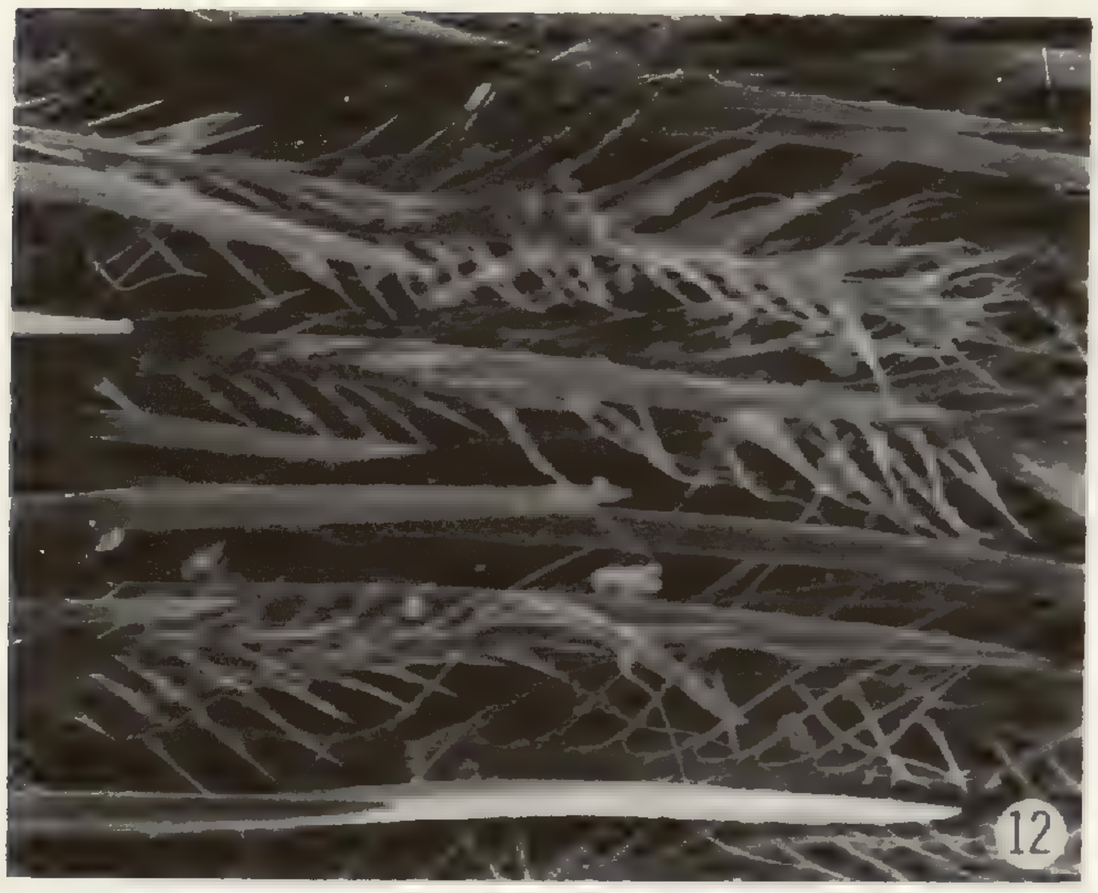
TABLE 2. Structures used in grooming and pollen manipulation in Apoidea. Symbols: + = present; ± = weakly developed; − = absent; footnotes identify limited occurrences of structures.

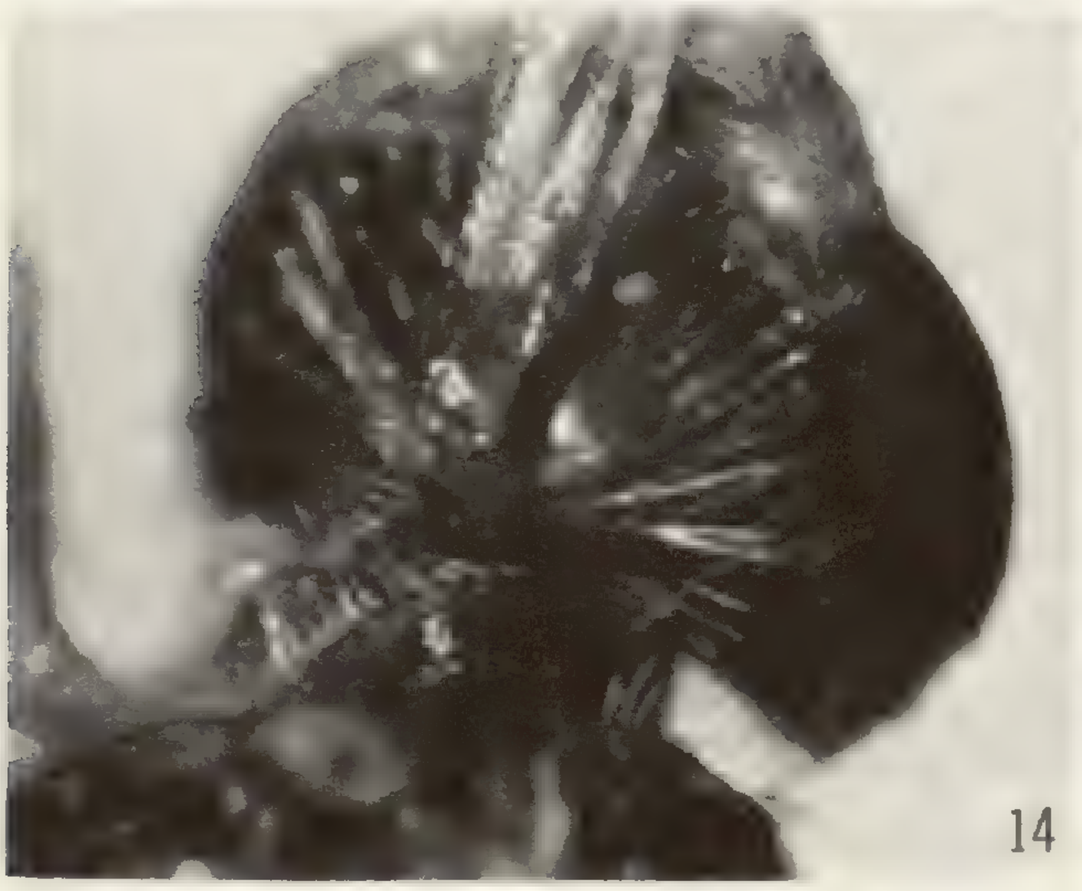
Location of Grooming Structures	Apoidea Families								
	Colletidae	Oxaeidae	Andrenidae	Halictidae	Melittidae	Fideliidae	Megachilidae	Anthophoridae	Apidae
Mouth parts									
Galea comb	+	−	+	+[e]	+[f]	−	−	±[l]	−
Stipes comb	−	−	−	−	−	−	−	+	+
Fore leg									
Antennal cleaner	+	+	+	+	+	+	+	+	+
Basitarsal brush and field (inner)	+	+	+	+	+	+	+	+	+
Mid leg									
Basitarsal brush (inner)	+	+	+	+	+	+	+	+	+
Tibial brush (outer apex)	+	+	+	+	+	+	+	+	+
Tibial comb (inner)	+	−	+	+	+[g]	−	−	−	−
Femoral comb (ventral base)	+[a]	−	+[c]	±	+[h]	−	−	−	−
Femoral brush (ventral base)	+[b]	+	+[d]	−	−	+	+[j]	+	−
Trochanteral brush (ventral)	±[b]	±	+[d]	−	+[i]	±	±[k]	+	+
Hind leg									
Basitarsal brush (inner)	+	+	+	+	+	+	+	+	+
Tibial brush and field (inner)	+	+	+	+	+	+	+	+	+

[a] *Colletes*.
[b] *Lonchopria* and *Caupolicana*.
[c] Panurginae.
[d] Andreninae.
[e] *Nomia* and *Corynura* (Jander, 1976).
[f] *Dasypoda* (Jander, 1976).
[g] Some *Hesperapis* and *Macropis* (Jander, 1976).
[h] *Hesperapis*.
[i] Melittini.
[j] Strong in Lithurginae, weak in Megachilinae.
[k] Weak in Megachilinae, absent in Lithurginae.
[l] *Ceratina* (Jander, 1976).

and hind leg scopae exemplify these regional morphogenetic fields (Pasteels & Pasteels, 1974, 1975, 1976, 1979) as do some grooming structures (Table 3). Hairs which form these fields appear to be derived from common body hairs.

The phylogeny of many grooming structures has been discussed by Grinfel'd (1969) and Jander (1976). The mouthpart combs that clean the fore legs of bees





FIGURES 12–15. Specialized hairs for transport and manipulation of oils, and extraction of hidden pollen.—12. Hind tibial scopa of *Exomalopsis* sp. with two types of hairs characteristic of oil collecting species (SEM) (200×).—13. Oil combs of fore (f) and mid (m) basitarsi of *Centris* sp.—14. Pollen extracting hairs on gena near proboscidial fossa of *Perdita bellula*—15. Labial palpae of *Proteriades jacinctana*. Photos 13–15 by D. L. Briggs.

and aid in ingestion of pollen are figured and discussed by Jander (1976). The antennal cleaner of the fore leg consists of the modified tibial spur and the notch of the basitarsus it opposes (Fig. 9). This structure occurs in both sexes throughout the higher Hymenoptera (Grinfel'd, 1969). The brush on the inner face of the fore basitarsus usually consists of unbranched setae with enlarged tips. This type of seta also often occurs apically on the inner face of the tibia (Fig. 9) forming a regional morphogenetic field (cf. Pasteels & Pasteels, 1973). Grinfel'd (1969) argued that the mid legs are more conservative than others due to the need for support on at least two adjacent pairs of legs when at rest and mentioned only the brush of the inner face of the mid basitarsus (Fig. 10) as a grooming tool. The mid basitarsal brush is universal among bees (Jander, 1976) and the best developed brushes have an oblique groove to receive and clean the fore leg with more efficiency than a flat brush. Jander (1976) also figures and describes opposing combs on the inner face of the mid tibia and the ventrobasally on the mid femur. The tibial comb is most extensive in Andrenidae and Halictidae, the two families that lack the oblique furrow of the mid basitarsus. In addition to the structures

TABLE 3. Specialized areas with hooked hairs for extracting pollen hidden within flower structures.

Bee Taxa	Family	Areas with Hooked Hairs	Pollen Host	Family	Source
Proteriades, most species	Megachilidae	Labial palpi 1–2	*Cryptantha*	Boraginaceae	Michener (1944)
Osmia, very few species	Megachilidae	Labial palpi 1–2	*Cryptantha*	Boraginaceae	Michener (1944)
Andrena (*Scoliandrena*) *osmioides* Cockerell and undescribed species	Andrenidae	Galea and prementum	*Cryptantha*	Boraginaceae	Michener (1944)
Calliopsis (*Verbenapis*), 4 species	Andrenidae	Fore tarsi	*Verbena*	Verbenaceae	Michener (1944)
Hesperapis elegantula group, 3 species	Melittidae	Mandibles, stipes, and gena near fossa	*Coldenia*	Boraginaceae	Stage (1966)
Perdita (*Heteroperdita*) *arenaria* Timberlake and 6 relatives	Andrenidae	Gena near fossa	*Coldenia* and *Heliotropum*	Boraginaceae	Stage (1966) & Timberlake (1954)
Hesperapis laticeps Crawford	Melittidae	Mandibles, stipes and gena near fossa	*Mentzelia* and *Eucnide*	Loasaceae	Stage (1966)
Megandrena (*Erythrandrena*) *mentzeliae* Zavortink	Andrenidae	Fore tarsi	*Mentzelia*	Loasaceae	Zavortink (1972)

Jander (1976) mentions, a prominent brush exists on the venter of the trochanter in many bees and may form part of a regional morphogenetic field with a brush on the base of the femur (Fig. 11). Brushes apically on the inner and outer faces of the mid tibia may also function in grooming. The hind leg contains brushes on the inner faces of the basitarsus (Fig. 8b) and the tibia. The latter brush is composed of spatulate or chisel-tipped nonbranching setae (Fig. 8w) that occur in all bees (Pasteels & Pasteels, 1972) (cf. Fig. 1D) and may extend as a regional morphogenetic field to the apical inner face of the femur. Special brushes ventrally on the mesepisternum, mid and hind coxae in many *Trigona* (Meliponinae: Apidae) function in pollen transfer (Michener et al., 1978).

Grooming and Pollen Manipulation Behavior

Studies of grooming and pollen manipulation behavior have often elucidated the structures involved and provided functional interpretations for those known only for their morphological detail. Hlavac (1975) identified two functional types of grooming structures: pressure-squeeze in which pressure applied to the tips of flexible setae squeezed together forces particles trapped between them outward (e.g., antennal cleaner of bees); and combs (single rows) or brushes (multiple rows) of slanted setae opposed by interdigitating bristles (e.g., basitibial brushes and the surfaces they clean). The two major types of interactions between grooming or pollen transfer structures involve scraping: contact only while the cleaner is moving in the direction its comb or brush setae are pointed (unidirectional); and rubbing: contact during both push and pull strokes resulting in alternate mutual cleaning of the parts rubbed (bidirectional) (Jander, 1976; Jander & Jander, 1978). Scraping movements are involved in pollen manipulation and packing. Rubbing movements terminate grooming by ridding the structures of debris. Thus, although Hlavac (1975) stated pollen collection is "grooming in reverse," this oversimplification applies only to the final movement of loading the pollen transport apparatus. Grooming behavior in most insects involves scraping of an area or structure with an appendage and then rubbing that appendage with its counterpart to get rid of debris. Pollen manipulation in bees requires integration of scraping cleaning behavior of a series of successive grooming structures to move pollen rearward to the transport apparatus. Loading the pollen transport apparatus involves the substitution of a scraping movement for the final rubbing motion that would shed any debris.

An exception to the rearward movement of pollen occurs in bees that have combs on the maxillary galea or stipes. In these bees the fore leg cleans the head and is in turn cleaned by a mouthpart comb (Jander, 1976). This aids in ingestion of pollen. This forward movement of pollen appears to be unique to bees possessing these combs and does not involve pollen cleaned from the rest of the body by the mid and hind legs (Michener et al., 1978).

The rearward sequence of pollen movement begins with the antennae being cleaned by the antennal cleaner of the fore leg. The basitarsal brush and field of the fore leg cleans most of the head and mouthparts. In most Anthophoridae it also cleans the thoracic dorsum (Jander, 1976). The fore leg is drawn between the folded mid leg. This is the most specialized leg cleaning motion in the Hymenoptera (Farish, 1972). The comb of the mid tibia and the comb of the base

of the mid femur scrape and remove pollen from the fore leg in the primitive bees (Jander, 1976). The outer apical brush of the mid tibia may groom the inner rear of the fore leg during the "elusive rudimentary" movement mentioned by Jander (1976). In many bees, especially Anthophoridae and Apidae, a brush on the venter of the trochanter scrapes pollen from the inner basitarsal brush of the fore leg, while the outer face of the fore leg is cleaned by the brush of the mid basitarsus. Pollen is scraped from the mid trochanteral brush and dorsum of the thorax by the brush of the mid basitarsus. Pollen concentrated in this latter brush is then applied directly to the hind leg scopa of most bees or the corbicula of most Meliponinae, or to the brush on the inside of the hind basitarsus in bees with abdominal scopae and Apidae with a well-developed auricle between the hind tibia and basitarsus (Michener et al., 1978). Wings are groomed between the side of the abdomen and the inner faces of the hind tibia and basitarsi with the hind leg as the primary cleaner of all wing surfaces and the abdomen laterally (Jander & Jander, 1978). However, my observations on grooming in honey bees suggest that only the brush of spatulate hairs of the inner face of the hind tibia and apex of the femur cleans the wings and lateral abdomen. Pollen is cleaned from these brushes by the opposite (contralateral) hind basitarsal brush. Pollen accumulated in the hind basitarsal brushes is scraped and packed into abdominal scopae or removed by the contralateral rastellum (Fig. 8) and moved to the outer face of the hind tibial corbicula in Apidae with a well-developed auricle (Fig. 7). Pollen on the hind basitarsal brush in other bees cannot be packed in the pollen transport apparatus, but may not be rubbed off until the female unloads pollen in her brood cell.

Pollen packing in the corbicula of *Apis* has been well described by Casteel (1912) and Hodges (1952), and of *Bombus* by Sladen (1912). Basically, pollen is scraped from the opposite hind basitarsal brush by the rastellum and accumulates behind the rastellum. It is forced up and out onto the corbicula by the auricle as the tibiobasitarsal joint is closed. The single hair on the corbicula in *Apis* is assumed to play a role in securing the pollen load (Casteel, 1912; Hodges, 1952) and a similar role is suggested for the two or three hairs at the "entrance to the corbicula" in *Bombus* (Sladen, 1912). Legge & Bole (1975) noted variations in position of the single hair in honey bees and suggested that it was not essential for the formation of pollen loads since it was absent or too close to the posterior border in some bees to be functional. Hodges (1967) removed the single hair from one corbicula of two bees and found that the pollen load on the corbicula without the hair was smaller (about one-third the weight) than that on the corbicula of the leg with the hair. Witherell (1972) found that a small proportion of hairless mutant workers were able to gather small oddly positioned pollen loads despite the lack of the single corbicular hair and with only 5–10% of normal body hair. Thus, although the absence of the single corbicular hair does not completely prohibit formation of pollen loads, it is evident from the last two studies that the hair is important in the formation of a normal full pollen load.

Michener et al. (1978) have critically compared pollen manipulation in the family Apidae and described the types of pollen packing behavior. The placement of pollen directly onto the corbicula by the mid legs (Type I) that occurs rarely in some *Trigona* (Meliponinae) collecting large sticky *Cucurbita* pollen is similar to the manner most bees load the scopa of the hind leg. The application of pollen

on the outside of the tibiotarsal joint and the subsequent pushing it basad on the corbicula by scraping the hind leg along the mid leg and by flexing the basitarsus (Type II, ipsilateral) is characteristic of many Meliponinae and probably Euglossini. Pollen may be scraped from the brush on the inner face of the hind basitarsal brush by the rastellum of the opposite leg and pushed through the auricle onto the outer face of the corbicula (Type II, contralateral) in *Apis*, *Bombus*, and rarely in Melioninae. The corbicular structure and pollen packing behavior along with other derived characters was used by Winston & Michener (1977) to show the phylogenetic distinctness between Meliponinae and Apinae.

The loading of nesting materials (e.g., mud, resins, cerumen, etc.) in the corbicula of Meliponinae, Apinae, and Euglossini and the collection of aromatic compounds by male Euglossini are similar to Type I pollen packing (Michener et al., 1978).

When a pollen-laden female returns to her nest, the pollen is deposited in a brood cell presumably by a final grooming motion. Removal of pollen loads in the brood nest has not been well studied since relatively few bees have been studied in observation nests. *Apis* and *Bombus* workers extend the hind legs into a pollen storage cell and simultaneously remove both pollen pellets from the corbiculae with their mid basitarsi. Even *Apis* that have lost their pollen loads in a trap at the hive entrance will complete deposition behavior before returning to forage (McDonald, 1968). Bees transporting dry pollen in scopae presumably scrape pollen from the scopa with the structure used in loading the scopa (i.e., mid or hind basitarsal brushes) and remove it by rubbing opposing brushes of each leg pair. The mid basitarsal brushes may also be scraped by the hind basitarsal brushes which are then rubbed together to deposit pollen in the brood cell.

Foraging Behavior

Bees exhibit many other behavioral adaptations in foraging behavior that facilitate the collection of pollen in addition to those already discussed for packing pollen for transport (modification of grooming behavior) and for overcoming structural limits to size of pollen grains that can be packed (e.g., moistening pollen). Many of these behaviors involve some degree of learning or modification of behavior to fit specific situations.

FLORAL CONSTANCY

Most bees exhibit a high degree of constancy to floral species at the individual level when foraging for pollen (Grant, 1950; Linsley, 1958; Free, 1963, 1970). This increases foraging efficiency and exploitation of a rewarding resource by reducing time and effort involved in learning to locate new sources and to manipulate diverse floral mechanisms. Efficiency in exploiting floral resources by eusocial Apidae is further enhanced by elaborate dance communication in *Apis* (von Frisch, 1967; Lindauer, 1967); by trail marking in Meliponini (Lindauer, 1967; Esch, 1967); and by constantly monitoring the changing floral community through a process of majoring and minoring (Heinrich, 1976; Oster & Heinrich, 1976) in bumble bees since they lack the ability to communicate food source location to their hive mates.

Constancy to pollen sources at the population and species level is called oligolecty (Robertson, 1925). Linsley & MacSwain (1958) define oligolectic species as those "in which the individual members of the population, throughout its range and in the presence of other pollen sources, consistently and regularly collect pollen from but a single plant species or a group of a similar or related plant species, turning to other sources, if at all, only when there is a local shortage or absence of that pollen." The origin of this type of host specificity was hotly debated by Robertson (1912, 1914, 1925) and Lovell (1912, 1913, 1914, 1918). Robertson suggested oligolecty arose from interspecific competition while pollen was limiting. Lovell argued that there were always sufficient supplies of pollen, but that individuals specializing on a pollen source were more efficient and therefore produced more progeny. However, the two hypotheses are not necessarily mutually exclusive. During times of pollen stress the species with individuals that compete best for the limited pollen available from a plant species will leave the most progeny. During periods of pollen abundance those individuals most efficient at obtaining pollen from the plant host will leave the most progeny. Thus, the two mechanisms may reinforce each other, enhancing the rate of evolution toward host specificity. Some bees may survive interspecific competition by specializing on plants unattractive to others due to unusual floral characteristics such as pollen larger than average size, hidden from most visitors, presented only during unusual and restricted periods, or held together in webby masses by viscin threads.

Oligolecty occurs at levels of organization above the species, including the subgenera *Onagrandrena, Diandrena* (*Andrena*: Andrenidae) (Linsley et al., 1963a, 1963b, 1964, 1973; Thorp, 1969; MacSwain et al., 1973) and *Sphecodogastra* (*Lasioglossum*: Halictidae) (Linsley et al., 1963b; Kerfoot, 1967b); the genera *Hesperapis* (Melittidae) (Stage, 1966), *Proteriades* (Megachilidae) (Timberlake & Michener, 1950), *Diadasia* (Anthophoridae) (Linsley & MacSwain, 1957, 1958) and *Xenoglossa* (Anthophoridae) (Hurd & Linsley, 1967). Although all members of some of these taxa are oligolectic on single plant genera or families (e.g., *Xenoglossa* on *Cucurbita, Andrena* (*Onagrandrena*) on Onagraceae) some contain species oligolectic on distinctly different plant hosts from their relatives. Thus, most *Diandrena* are oligolectic on Onagraceae (10) or ligulate Compositae (10) while others are oligolectic on nonligulate Compositae (3), *Ranunculus* (1), and *Arenaria* (1) (Thorp, 1969); similarly most North American *Diadasia* are oligolectic on Malvaceae (14) while others are oligoleges of *Opuntia* (3), *Convolvulus* (1), *Clarkia* (1), and *Helianthus* (1) (Linsley & MacSwain, 1957). Verbal models to account for speciation and host shifts within higher taxa of oligolectic bees have been proposed by Linsley & MacSwain (1957, 1958), Thorp (1969), and Cruden (1972).

Bees not only express fidelity to crop species, but also to areas within a crop (Singh, 1950; Thorp, unpubl.). They tend to forage through the crop in the most economical pattern, e.g., tending to visit nearest-neighbor flowers (Levin & Kerster, 1969) and to fly in the direction of their previous flight (Levin et al., 1971). Smaller more host specific bees tend to fit near-neighbor foraging models more closely than larger polylectic bees (Estes, Thorp & Briggs, unpubl.).

SEASONAL SYNCHRONY

Oligolecty usually involves close seasonal synchrony between the flight period of the adult bee and the bloom period of its pollen hosts (Robertson, 1929) based on observations at the flower. However, there may be considerable variation from season to season when first emergence of bees from their nests is related to first bloom (Linsley, 1958). Still, seasonal synchronization remains reasonably close. The extrinsic stimuli and intrinsic responses that govern this synchrony are not well understood, especially since the environments of the plant and bees are quite different (Linsley, 1958). The seasonal appearance of a vernal oligolectic bee (*Hesperapsis*: Melittidae) and the flowers of its pollen host (*Geraea*: Compositae) in October following unseasonal rains of more than 25 cm in the Colorado Desert of California (Hurd, 1957) is strong supportive evidence that the plant and the bee respond ultimately to the same extrinsic stimuli. There is evidence that both plants and bees can holdover unfavorable seasons and delay their appearance up to two years, e.g., an *Andrena* (Andrenidae) oligolectic on *Limnanthes* (Limnanthaceae) and a polylectic *Trachusa* (Megachilidae) during the 1975–1976 drought years in California (Thorp, unpubl.). The foregoing suggests moisture is the critical extrinsic stimulus; however, it is well known that temperature is the critical factor determining emergence of the alfalfa leafcutting bee, *Megachile rotundata* (Fabricius). Most bees of seasonal environments (temperate, and semiarid tropical) holdover the unfavorable parts of the year in diapause (physiological arrestment) in their natal cells as adults (many vernally active species) or more often as postdefecating larvae. This physiological adaptation is an important part of the mechanism for synchronizing bloom and bee activity seasonally.

LOCATING POLLEN SOURCES

Once a female bee has emerged, mated, and constructed her nest to the proper stage, she must locate a pollen source. Flowers produce a wealth of recognition cues, e.g., chemical, visual, and even tactile that correspond to the sensory capabilities of bees and other pollinators. Bees even perceive some cues man does not (e.g., ultraviolet patterns) (Lutz, 1924; Daumer, 1956, 1958; von Frisch, 1967). Many of these cues are used by bees to recognize and discriminate rewarding from nonrewarding flowers, but which, if any, of these stimuli elicit innate responses attracting naive bees has not been well demonstrated. Chemical stimuli may be most important, since the only experience a newly emerged solitary bee has had with an appropriate pollen source is the pollen in its natal cell (Linsley, 1958). In this regard specific chemicals of pollen may serve as attractants (Stanley & Linskens, 1974) or at least recognition cues for bees. A pollen lipid has been identified as attractive to honey bees (Lepage & Boch, 1968; Hopkins et al., 1969, 1975). This preimaginal conditioning to pollen odors assumes an important role in reinforcing intrinsic adaptations associated with the host specificity and in the model proposed by Thorp (1969) to account for host switches among species of oligolectic taxa.

Evidence that suggests a brief period of searching and learning is involved in finding the proper pollen source comes from *Andrena* (*Onagrandrena*) *linsleyi*

TABLE 4. Examples of daily synchrony between oligolectic bees and their pollen hosts.

Daily Period[a]	Bee Taxa	Family	Pollen Host	Family	Source
Matinal	*Andrena* (*Onagrandrena*) *mojavensis* Linsley & MacSwain and 5 relatives	Andrenidae	*Camissonia*	Onagraceae	Linsley et al. (1964)
	Andrena (*Diandrena*) *chalybaea* (Cresson) and 8 relatives	Andrenidae	*Camissonia*	Onagraceae	Thorp (1969)
	Andrena (*Diandrena*) *chalybioides* (Viereck) and 7 relatives	Andrenidae	*Agoseris*	Compositae	Thorp (1969)
	Hemihalictus lustrans (Cockerell)	Halictidae	*Pyrrhopappus*	Compositae	Estes & Thorp (1975)
	Xenoglossa, all 7 species, and *Peponapis*, all 13 species	Anthophoridae	*Cucurbita*	Cucurbitaceae	Hurd & Linsley (1970)
Late Afternoon	*Andrena* (*Onagrandrena*) *rozeni* Linsley & MacSwain	Andrenidae	*Camissonia*	Onagraceae	Linsley et al. (1963a, 1963b)
	Andrena (*Onagrandrena*) *vespertina* Linsley & MacSwain	Andrenidae	*Camissonia*	Onagraceae	Linsley et al. (1973)
Matinal & Late Afternoon	*Andrena* (*Onagrandrena*) *raveni* Linsley & MacSwain	Andrenidae	*Camissonia*	Onagraceae	Linsley et al. (1963b)
	Lasioglosssum (*Evylaeus*) *galpinsiae* Cockerell	Halictidae	*Oenothera*	Onagraceae	Bohart & Youssef (1976)
Crepuscular & Nocturnal	*Perdita* (*Xerophasma*) *pallida* Timberlake *bequaertiana* Cockerell	Andrenidae	*Oenothera*	Onagraceae	Linsley et al. (1963a); Kerfoot (1967a)
	Lasioglossum (*Sphecodogastra*) *texanum* (Cresson) *noctivagum* Linsley & MacSwain	Halictidae	*Oenothera*	Onagraceae	Linsley et al. (1963b); Kerfoot (1967b)
	Megalopta centralis	Halictidae	*Solanum*	Solanaceae	Linsley et al. (1963b); Kerfoot (1967b)
Diurnal	*Andrena* (*Diandrena*) *submoesta* Viereck *puthua* (Cockerell)	Andrenidae	*Lasthenia*	Compositae	Thorp (1969)

TABLE 4. Continued.

Daily Period[a]	Bee Taxa	Family	Pollen Host	Family	Source
	Andrena (*Diandrena*) *lewisorum* Thorp	Andrenidae	*Clarkia*	Onagraceae	Thorp (1969)
	Hesperapis regularis (Cresson)	Melittidae	*Clarkia*	Onagraceae	MacSwain et al. (1973)
	Megachile (*Derotropis*) *gravita* Mitchell *pascoensis* Mitchell	Megachilidae	*Clarkia*	Onagraceae	MacSwain et al. (1973)
	Diadasia angusticeps Timberlake	Anthophoridae	*Clarkia*	Onagraceae	MacSwain et al. (1973)
	Diadasia enavata (Cresson)	Anthophoridae	*Helianthus*	Compositae	Hurd et al. (1980)
	Svastra obligua expurgata (Cockerell)	Anthophoridae	*Helianthus*	Compositae	Hurd et al. (1980)

[a] Daily periods as defined by Linsley & Cazier (1970).

Timberlake (Linsley et al., 1963a). This bee is an oligolege on the nocturnal blooming *Oenothera* on which it forages for residual pollen in the early morning. Early in their activity season females forage for pollen in the morning and afternoon on *Oenothera* and late afternoon opening species of the related *Camissonia*, but as the bloom of the former increases, the females of *A. linsleyi* shift their foraging to the preferred *Oenothera* in the early morning.

DIURNAL SYNCHRONY

Flowers often present pollen at specific and limited times of day and many bees adapt their foraging period for daily synchrony with their host. Many oligolectic bees and their host plants are matinal, a few are late afternoon, or crepuscular or nocturnal, and some are active all day (Table 4). Even within limited daily foraging periods a complex of oligolectic bee species may further partition a pollen resource with distinctly separated diurnal peak foraging times although their total foraging periods overlap, e.g., matinal *Andrena* (*Onagrandrena*) and *A.* (*Diandrena*) on *Camissonia* (Linsley et al., 1964, 1973; Thorp, 1969). Thorp (1969) found two sites with 8–12 species of *A.* (*Diandrena*) with six species each coexisting on the same species of *Camissonia*. The division is often related to adaptations of size and color with the largest and darkest forms visiting earliest in the day (Thorp, 1969; Linsley, 1978). Similar patterns occur with groups of polylectic species adapted to matinal plants such as *Solanum* (Linsley & Cazier, 1963; Bowers, 1975), *Cassia* (Thorp & Estes, 1975).

Some bees regularly forage both morning and late afternoon, e.g., oligolectic *Andrena* (*Onagrandrena*) *raveni* Linsley & MacSwain (Linsley et al., 1963b) and polylectic Caupolicanini (Linsley & Cazier, 1970). Other bees apparently learn proper timing, e.g., *Andrena linsleyi* (Linsley et al., 1963a). Knerer & MacKay (1969) found that oligolectic *Lasioglossum* (*Evylaeus*) *oenotherae* (Stevens) females shifted their foraging period on *Oenothera* from morning and evening to morning only after a brief learning period.

The time sense of honey bees has been demonstrated frequently (Ribbands, 1953; von Frisch, 1967). This sense permits honey bees to return to a food source in synchrony with its presentation. Usually some bees will arrive early each day. As food is successfully collected and returned to the hive, bees that have had experience with the crop are stimulated to forage by the odor of the incoming food. This type of conditioned response (Wenner & Johnson, 1966) can be used in training experiments, since introducing a training odor into the hive will stimulate trained bees to return to the training arena (Gary & Witherell, 1971). New recruits are directed to the crop by dance communication and odor.

Most polylectic and many oligolectic bees are associated with diurnal plants that have pollen available all day long, e.g., *Clarkia* (MacSwain et al., 1973); *Larrea* (Hurd & Linsley, 1975) and *Helianthus* (Hurd et al., 1980). These bees usually divide the diurnal foraging period into overlapping periods based on consistent differences in behavior (Linsley, 1978). Thus, Hurd & Linsley (1975) identified four diurnal foraging patterns of bees on *Larrea*: early morning and early afternoon; early to mid morning; mid morning to late afternoon; and throughout much of the day.

Diurnal synchrony of foraging by bees with pollen presentation of their hosts

appears to be primarily learned behavior. It may be delayed by extrinsic factors such as cloud cover, fog, or rain, but is often resumed in the same synchronous sequence when the weather ameliorates (Thorp, 1969; Estes & Thorp, 1975; Linsley, 1978). Bees may possess special structural adaptations, e.g., enlarged ocelli of crepuscular or nocturnal bees (Kerfoot, 1967a) or behavioral mechanisms, e.g., thermoregulation (Heinrich, 1974) that permit flight at lower light intensities or lower temperatures than their relatives are capable of.

RESPONSES TO UNUSUAL POLLEN PRESENTATION

Bees often exhibit special behavioral adaptations to unusual modes of pollen presentation or to material with pollenlike characteristics. Anthers of about 544 genera and an estimated 15,000–20,000 species of flowering plants dehisce through apical pores. Representatives of 444 of these genera may require vibratory behavior by bees to release pollen (Buchmann, 1978). Bees grasp apically pored anthers and vibrate them making an audible buzz by shivering the indirect flight muscles of the thorax. This shivering is adapted from normal flight, but with the wings remaining reflexed over the abdomen and is used in thermoregulation as preflight warm-up. This application of shivering behavior not only releases pollen from anthers with apical pores onto the bee where it can be groomed and packed, but also elevates the temperature of the bee, a useful by-product for early morning foragers (Bowers, 1975; Thorp & Estes, 1975). Some flowers with nonporicidal anthers are vibrated by their visitors, e.g., a *Melampyrum* (Scrophulariaceae) (Meidell, 1944) and a *Pedicularis* (Scrophulariaceae) (Macior, 1968).

The pollen grains of most buzz-pollinated flowers are usually small, unsculptured, and without pollenkitt (Buchmann & Hurley, 1978). Thus it is not surprising that in the complex of bees on *Solanum* studied by Linsley & Cazier (1963) most had dense scopae or added oil or nectar to the pollen loads.

In addition to buzzing apically dehiscent anthers, bees may also milk them by grasping an anther near its base with the mandibles and pulling apically (Thorp & Estes, 1975). Biting anthers with the mandibles is not an uncommon method among bees to release more pollen. However, biting their way into an unopened flower to collect pollen from anthers that dehisce just prior to anthesis (floral opening) is rare, but has been reported for a *Perdita* on *Proboscidea* (Hurd & Linsley, 1963). Although most zygomorphic flowers present their pollen so that it will be distributed either nototribically or sternotribically (Macior, 1974), some bees that are not the proper size to pick up pollen the proper way may modify their behavior, e.g., due to the size disparity between small bees like *Panurginus* and the large flowers of *Downingia bacigalupii*, the anther column does not contact the bee nototribically as in most other *Downingia* species so the bee collects pollen sternotribically while hanging upside down at the end of the column (Thorp, 1976). Some bees also may learn to operate special trip or trigger mechanisms to make pollen more readily available for collection, such as the trigger hairs of *Downingia* (Thorp, 1976). Bees, especially of the family Apidae, will sometimes collect pollen from anemophilous plants (Bogdan, 1962; Soderstrom & Calderón, 1971; Pojar, 1973). Honey bees frequently collect corn pollen and occasionally other pollenlike materials, such as rust spores (Chapman, 1964), feed mill dust, and sawdust. Some bees glean pollen that has fallen from the

anthers onto other floral parts (Wille, 1963). Females of *Trigona* (*Scaura*) exhibit morphological and behavioral adaptations for gleaning pollen from flower parts and leaves (Michener et al., 1978). A few bees will even collect pollen from the body surface (Laroca & Winston, 1978) or the scopae of other bees (Thorp & Briggs, 1979).

CONCLUSIONS

Bees exhibit many adaptations for the acquisition, manipulation, and packing of pollen for transport to their brood nests. These include structures that may not be modified from those normally used in grooming to the unique scopae and corbiculae evolved for the transport of the dustlike material, pollen, that serves as brood food for bees. These unique structures also may be used to transport other food materials such as oils, or to transport nesting materials such as mud, resin, or cerumen. Scopal hairs may show further modification in their spacing and amount of branching in relation to the size and structure of the pollen grains they normally carry. Other special hair groups have evolved in some bees for the extraction of cryptic pollen and the manipulation of plant oils. Enlarged ocelli are present in many bees which forage at periods of low light intensity.

Physiological adaptations include diapause during unfavorable parts of the year and for holding over unfavorable years so that bees can be seasonally synchronized with their pollen sources. Time sense makes possible daily synchrony with specific pollen presentation periods. The shivering mechanism for thermoregulation in some permits flight at low temperatures, and is sometimes applied in releasing pollen from buzz-pollinated plants. The general visual, chemical, and tactile senses are attuned to the recognition cues presented by plants, including the ability to see ultraviolet patterns invisible to man.

Behavior patterns, including grooming, adding nectar to pollen loads, host specificity, preimaginal conditioning, interfloral flight patterns, adaptability in responding to diverse structures and modes of pollen presentation, can be applied to new situations and be used to modify innate structural and physiological adaptations. Most of the behavioral patterns involve learning which promotes considerable flexibility in response to new situations. Fidelity to area, near-neighbor, and directional foraging have important effects on the genetic structure of plant populations.

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POLLEN WALLS AS ADAPTIVE SYSTEMS[1]

J. HESLOP-HARRISON[2,3]

WALL STRUCTURE AND THE MANY DIMENSIONS OF ADAPTATION

The structural variation of angiosperm pollen is primarily related to the wall, for the male gametophyte itself is simple in organization and more or less uniform in character throughout the group. The division of the wall into an outer exine and an inner intine is clearly a fundamental feature, as it is in the pollen grains and spores of other vascular groups, but the relative development of the strata differs widely among the families. The exine, usually the more structurally complex of the wall layers, is strikingly diverse in the types of wall sculpturing it can express, as well as in the numbers, distribution, and architecture of apertures and internal cavities. Faced with such variation, the first impulse is assuredly to attempt to bring some order and understanding by classification and ordination, and this has been the aim of palynologists since the days of von Mohl, a century-and-a-half ago. As this present symposium has shown, the task is by no means complete; but what has been achieved is already impressive, not least in the contribution pollen taxonomy has made to the advance of angiosperm taxonomy in general. If one's inclination is to ask for explanations, however, classification is not enough. The instinct is to seek for physiological meaning in the pollen grain wall—to attempt to understand what functions the structural features fulfill in the general biology of plants, and to search for some comprehension of the variation in form in evolutionary terms, seeking for evidence of adaptive diversification.

The essential function of the pollen grain and the tube that emerges from it is, of course, to deliver a pair of gametes to the embryo sac. The haploid male gametophyte with its single vegetative cell is structurally simple, but the attainment of its functional objective, the double fertilization, demands considerable physiological sophistication. This is expressed in a whole sequence of interlocking adaptations associated with dispersal, interaction with the stigma and style, nutrition, growth, and target finding. We now know that in the journey between the anther and the receptive stigma a major role is played by the pollen grain wall, which is concerned not only with protection and dispersal, but with the hydrodynamics of the gametophyte within it, and also in various subtle ways in the interactions on the stigma. The wall, in fact, serves many functions; and this must mean that in the course of angiosperm evolution it has been the target of many kinds of selective pressure. To it, as to any adaptive structure, a familiar truism must apply, namely, that the result of evolution under manifold selective forces must in each of the surviving lineages represent some sort of a compro-

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mise—a compromise that has been proved successful by the very fact of survival, but which nevertheless may not be optimal for each individual function.

Undoubtedly this helps us to understand some of the diversity encountered among the pollens of living angiosperms, and the more so when another truism of biological adaptation is taken into account, namely, that the same functional end can usually be attained by different morphological or physiological devices. The implication of this is that the compromise reached in the pollen walls of one group may be different from that attained in another. All are successful in some degree, but none is likely to be perfect. And to this we may add the further probability: that each may have elements not readily interpreted in adaptive terms at all, being related to lineage and the evolutionary events of a remote past, or being simply the products of fortuitous change.

I make these comments before turning to my main theme to avoid possible misunderstandings. Serious difficulties *do* arise in trying to interpret the intimate details of pollen structure in an adaptive sense, and one must be wary of carrying zeal for such interpretation too far. Such details do not *have* to be adaptive at all; or do not have to be adaptive in present circumstances. After all, there is no reason why structural idosyncracies not subject to intense selective pressures should not be conserved while other features undergo evolutionary change. It has long been supposed that such conserved characteristics are not only valuable as taxonomic criteria but offer good guides to phylogenetic affinity—an article of faith with those concerned with pollen phylogeny, just as it is with those whose interest embraces the whole organism. But the overriding fact is that the major structural and other features of pollen grains are likely, in all groups, to reflect adaptive function; and here lies the challenge—to identify these features and seek out their roles, or *purposes*, as Darwin himself would not have hesitated to say. The investigation of functional adaptation has no less its fascinations than when Darwin wrote to Thiselton-Dyer in November 1880, "many . . . are very contemptuous about making out the use of organs; but they may sneer the souls out of their bodies, and I for one shall think it the most interesting part of natural history." In this spirit, then, let us consider the adaptive characteristics of the pollen wall.

THE WATER RELATIONS OF THE POLLEN GRAIN

The importance of pores and slits in the wall allowing pollen grains to change in volume was noted as long ago as 1834 by von Mohl, and several other authors of the 19th Century commented on aspects of this function, including Kerner (Kerner & Oliver, 1904) who graphically described the events accompanying pollen hydration and the part played by pores and furrows. Wodehouse (1935) discussed not only the geometry of apertures but also their functions, introducing the term *harmomegathy* to describe the structural adaptations concerned with accomodating to volume change. More recently harmomegathy has been discussed by Payne (1972), who provided an informative table describing apertural mechanisms in a dozen or so families.

The volume changes undergone by pollen grains are occasioned by the loss or gain of water, and it is in control of this that one of the main physiological functions of apertural mechanisms is to be found (Heslop-Harrison, 1971, 1975b).

We can now see that, although lacking the ultimate sophistication of stomata, they are no less effective for regulating the water relations of a single cell. Their action has to be considered through two phases of the life of the grain, during the period of partial desiccation immediately preceding dispersal from the anther, and during the subsequent period of rehydration on the stigma leading up to germination.

THE PHASE OF DESICCATION

Pollen grains vary considerably in their degree of hydration at the time of dispersal. Leaving aside those families in which pollination is actually through the medium of water, there are others with insect- or bird-borne pollens that are hydrated almost to the extent of a somatic parenchymatous cell—for example, certain species of Zingiberaceae and allied families. In the main, however, the grains when released are partly desiccated. The pollen of rye (*Secale cereale*, Gramineae), freshly shed from the anther, may lose up to 35% initial weight when air dried at 80–90°C. This is a high figure when one considers the proportion of fresh weight accounted for by the wall and stored starch and sugars, but it is nevertheless considerably lower than would be lost by a vacuolated somatic cell subjected to the same conditions. Lily pollen fresh from the anther may lose 20–25%, and the pollen of Compositae even less, as low as 15% in some instances. Pollen grains may therefore be dehydrated to the extent of dry seeds at the time of dispersal.

The abstraction of water from the grains occurs immediately before and during the dehiscence of the anther, and this and the drying out of the anther wall cells including the endothecium accounts for the often dramatic fall in anther fresh weight during the hours preceding anthesis (Linksens, 1967). After anthesis, desiccation usually proceeds further, but at a rate very much determined by pollen type, and particularly wall morphology. Grass pollens commonly lose 20% of their initial weight at normal temperatures and humidities within an hour of release, while pollens like those of many Liliaceae and Compositae, already substantially dehydrated before anthesis, show losses of only 2–5%.

To understand the function of apertures in this phase of the life of the pollen grain, three factors have to be taken into consideration,

(a) the pathways of water loss from the male gametophyte;

(b) the capacity of the exine to accommodate volume changes consequent upon water loss and in doing so to control the flow; and

(c) the part played by surface materials in sealing the grain as the equilibrium state is reached.

Setting aside for the moment inaperturate grains and those where the exine is incomplete or absent, it can be said that, in general, water passing in or out of the vegetative cell will have two alternative pathways, through the apertures, or through the nonapertural exine. Since the pathways are in parallel, the total wall resistance, R_w, will equal $\frac{R_a R_e}{R_e + R_a}$ where R_a is the resistance offered by the apertures and R_e that due to the exine. The relationship is comparable with that between stomatal and cuticular transpiration from the leaf.

For the exine in the nonapertural regions the resistance will depend on the

degree of porosity. Fine-structural investigations have revealed that many aperturate pollens have virtually continuous nexines. Compact sporopollenin is essentially impermeable to water, so that where this is true the underlying intine is sealed from water loss or gain. In other pollens, the nexine is penetrated by fine channels, as for example in the grasses (Rowley, 1960). The function of these channels is unknown in any experimental sense, but physical considerations indicate that while there is a continuous liquid phase between intine, exine, and the aqueous environment of the loculus of the undehisced anther, water would be readily extractable through channels the dimensions of those of the grasses, 15–30 nm in diameter, the resistance being only that offered to flow through fine passages.

As for the apertural sites, they, characteristically, are areas of the wall where the exine is much reduced, or virtually absent. Illustrations of apertural exines have been given, for example, by Roland (1966, 1968). These show a variety of states, with sporopollenin deposited in granules or thin plates, very often with marked discontinuities. The intine is thus much more exposed at the apertural sites, presenting a surface that is therefore much less protected from water loss than elsewhere.

The intine itself has many of the chemical and structural characteristics of the primary wall of a normal somatic cell (Sitte, 1953). Like all walls of a pectocellulosic character, it is likely to be freely permeable to diffusing water, and will not therefore offer a serious resistance to water passing into or out of the vegetative cell. Moreover, apart from slight variation in thickness, usually at the apertural sites, the intine invests the grain more or less uniformly. Accordingly, the resistances in the two parallel pathways, through the apertures and through the exine, can be related to the areas of exposed intine; in general, the ratio $\frac{R_a}{R_e}$ will equal $\frac{A_e}{A_a}$, where A_e is the area of intine in communication with external water through the exine channels, and A_a the area in contact through the apertures. For most pollen types, A_a will considerably exceed A_e, emphasizing the importance of the apertural pathway, which will be the only one when the exine is impermeable.

During the first period of partial dehydration in the anther, the developing pollen lies immersed in the locular fluid. Water will be withdrawn along water potential gradients occasioned by deficits developed elsewhere in the anther, filament or receptacle. In many pollens, of which those of the Liliaceae and Gramineae provide good examples, starch accumulates at this time, and this will presumably steepen the gradient by sequestering osmoticum and raising the water potential.

The rate of water loss will be determined by the resistance offered by the pollen wall, and the control of exposed intine area at the apertures will be a crucial factor. It is in the regulation of this that the apertural mechanisms play their part during the phase of dehydration. The devices are diverse, but all are related to the change in volume of the grain during desiccation (Heslop-Harrison, 1971). A classification of some of the more important mechanisms is given in Table 1. All serve to reduce the area of the intine in contact with the locular fluid during dehydration and contraction; they act therefore to increase R_a and so

TABLE 1. Some examples of apertural mechanisms.

Exine Type	Sealing Devices
Colpate; sulcate	(a) Infolding, with buckling, folding or interleaving shutters; lipid seal (e.g., *Lilium*)
Porate	
Single pore	Operculate; no lipid seal (Gramineae)
Multiple pores	(a) Operculate; with or without lipid seal (e.g., Caryophyllaceae) (b) Occlusion by sporopollenin granules; lipid seal (e.g., Malvaceae)
Colporate; triaperturate	Infolding, with simple folding or buckling shutters or interleaving sporopollenin plates; with or without lipid seal (commonest dicotyledonous types)
Inaperturate	Granulate exine; lipid seal (e.g., many Iridaceae)

progressively to restrict water flow. At some point, however, the continuity of the liquid phase in the loculus will be broken, usually shortly before, or at the time of, the dehiscence of the anther. The pollen grains then find themselves in an aerial environment; and certainly by the time of release this establishes a new situation where the forces withdrawing water are not those imposed by water potential gradients in the stamen but by those of evaporation, many times greater in magnitude. The capillary forces holding water in channels as narrow as those found in the exine when this is porous are such as to ensure that they will not empty before the water content of the adjacent intine has reached an extremely low level. However, the menisci formed between the sporopollenin plates and granules at apertural sites may well have larger effective dimensions, and under the evaporative forces likely to be encountered on a normal day the air-water interface might be expected to withdraw to the nearest intine surface, where evaporation would be from the interfibrillar spaces. This would no doubt reduce the hydraulic conductivity still further, but loss would still be rapid and could lead very quickly to a lethal degree of desiccation.

This is resisted by still another adaptation, for it is in the control of water loss during the period immediately following the exposure of the pollen that lipid surface materials make one of their most important contributions. These lipidic materials are synthesized in the tapetum and transferred to the exine during the final period of pollen maturation. They show a marked selectivity in the walls to which they adhere (Heslop-Harrison, 1968). In *Lilium*, for example, they disperse preferentially over the spaces between the muri of the reticulate exine, and particularly over the colpus. In the latter site a globule is usually entrapped as the margins draw together during the final dehydration of the grain. This selective affinity may indicate the presence of a lipoprotein which forms an interfacial layer over the residual polysaccharide of the primexine matrix in the meshes of the exine reticulum, and over the intine itself where this is exposed.

The consequence of the coating of the exine and apertural sites with lipid is dramatic, for such a coating both seals the micropores of the exine where these are present and contributes greatly to increasing the hydraulic resistance of the

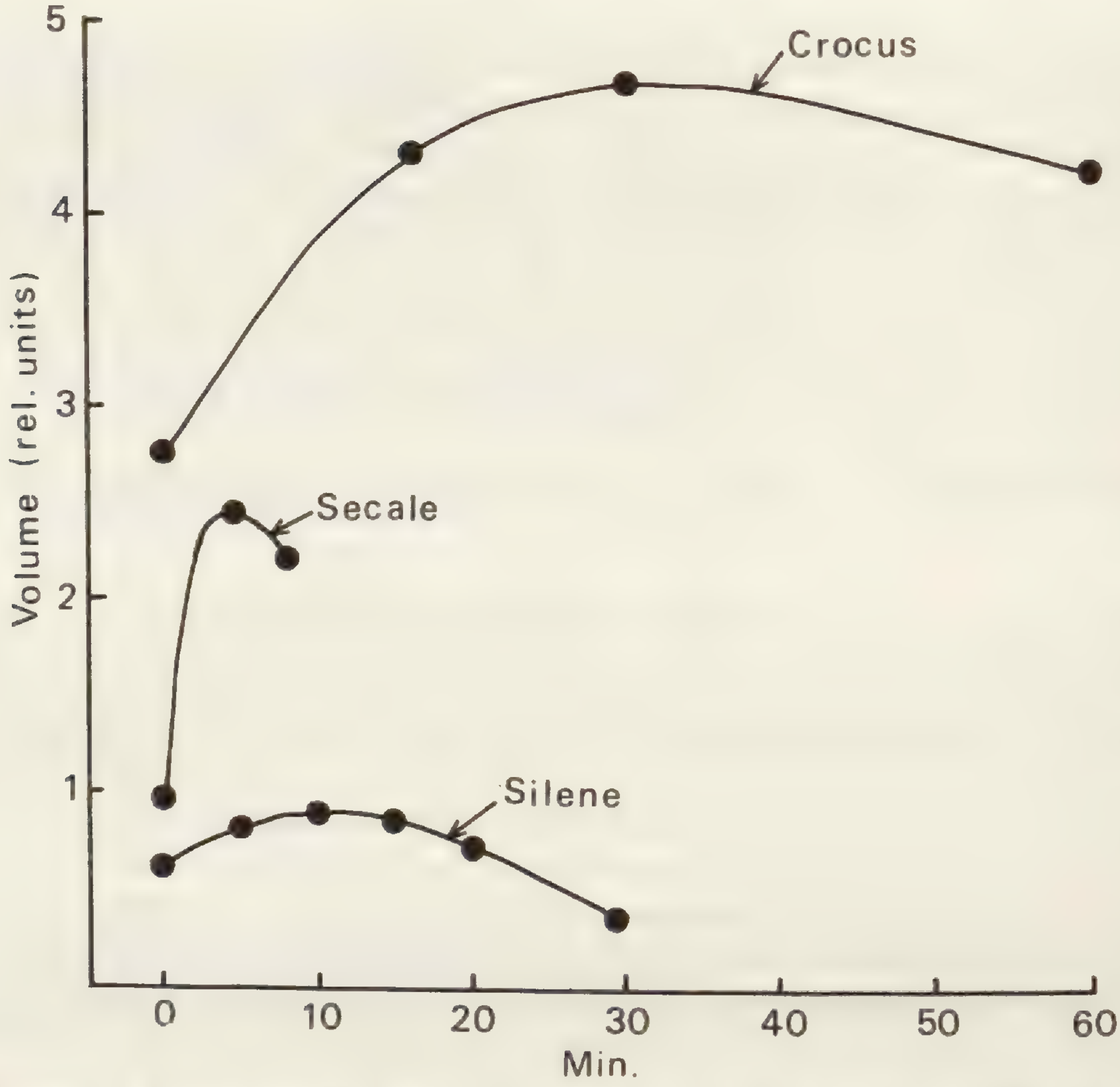


FIGURE 1. Volume changes during hydration in the pollen of *Crocus chrysanthus* (Iridaceae), *Secale cereale* (Gramineae), and *Silene vulgaris* (Caryophyllaceae). In all instances the volume of the grain itself is recorded; the tubes emerged at the point of maximum volume in each.

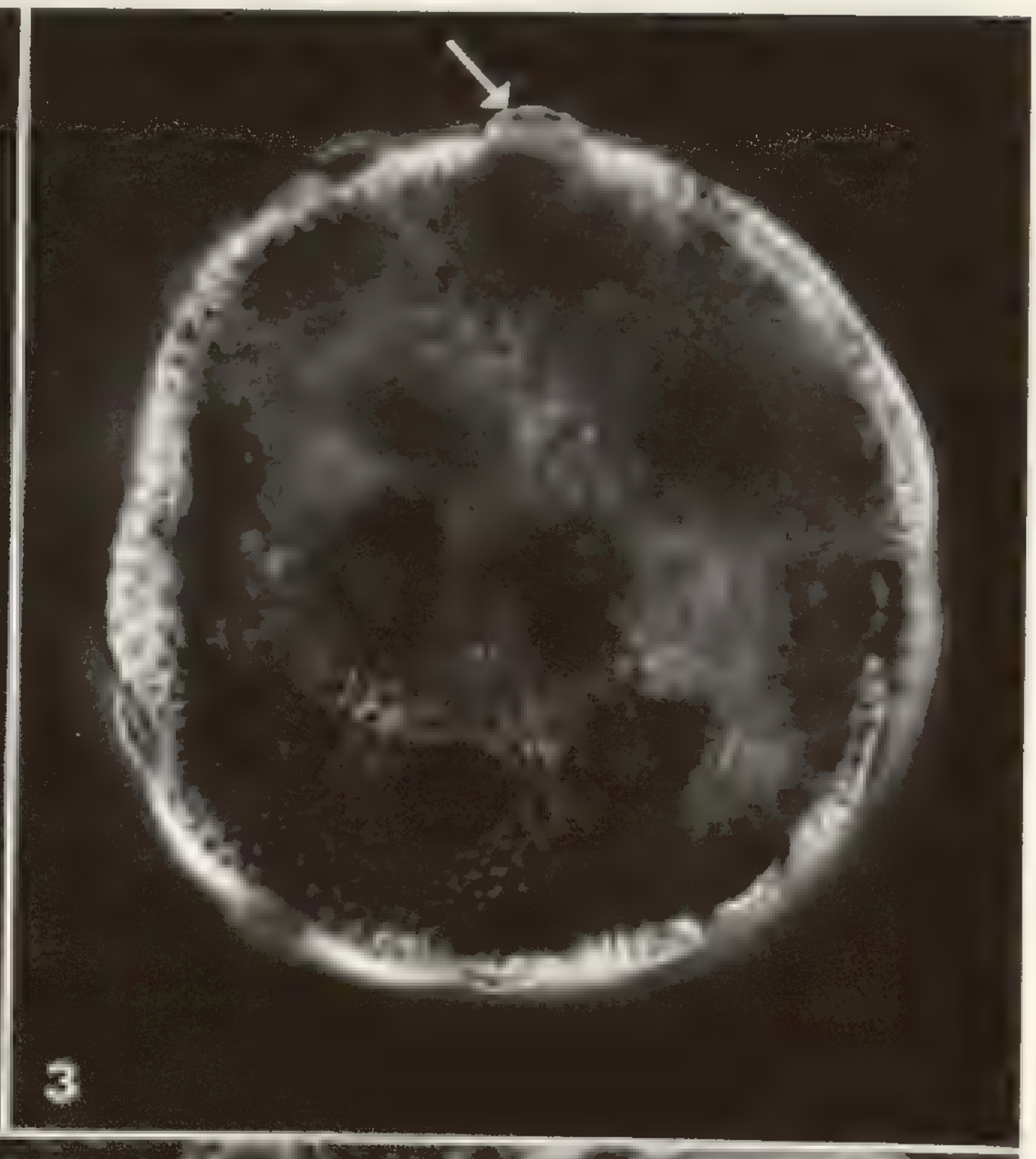
aperture sites. It is significant, therefore, that lipidic surface materials are present in most pollens. The exceptions, where the surface carries little surface lipid, are cases where the pollen is dispersed through water or saturated atmospheres—or where the pollen does indeed dehydrate quickly after release and has a very short functional life, as in the grasses and certain other wind pollinated groups.

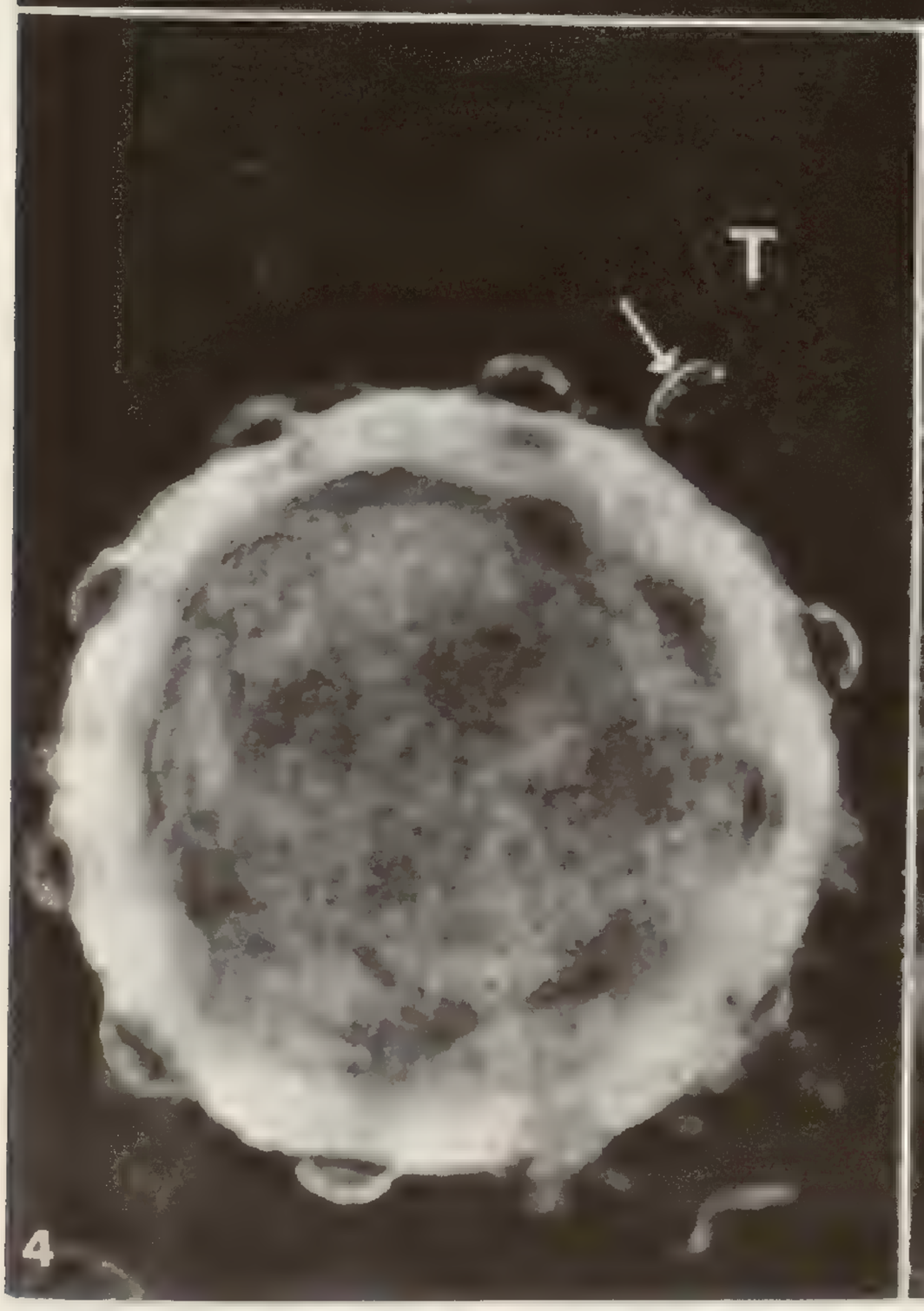
THE PHASE OF REHYDRATION

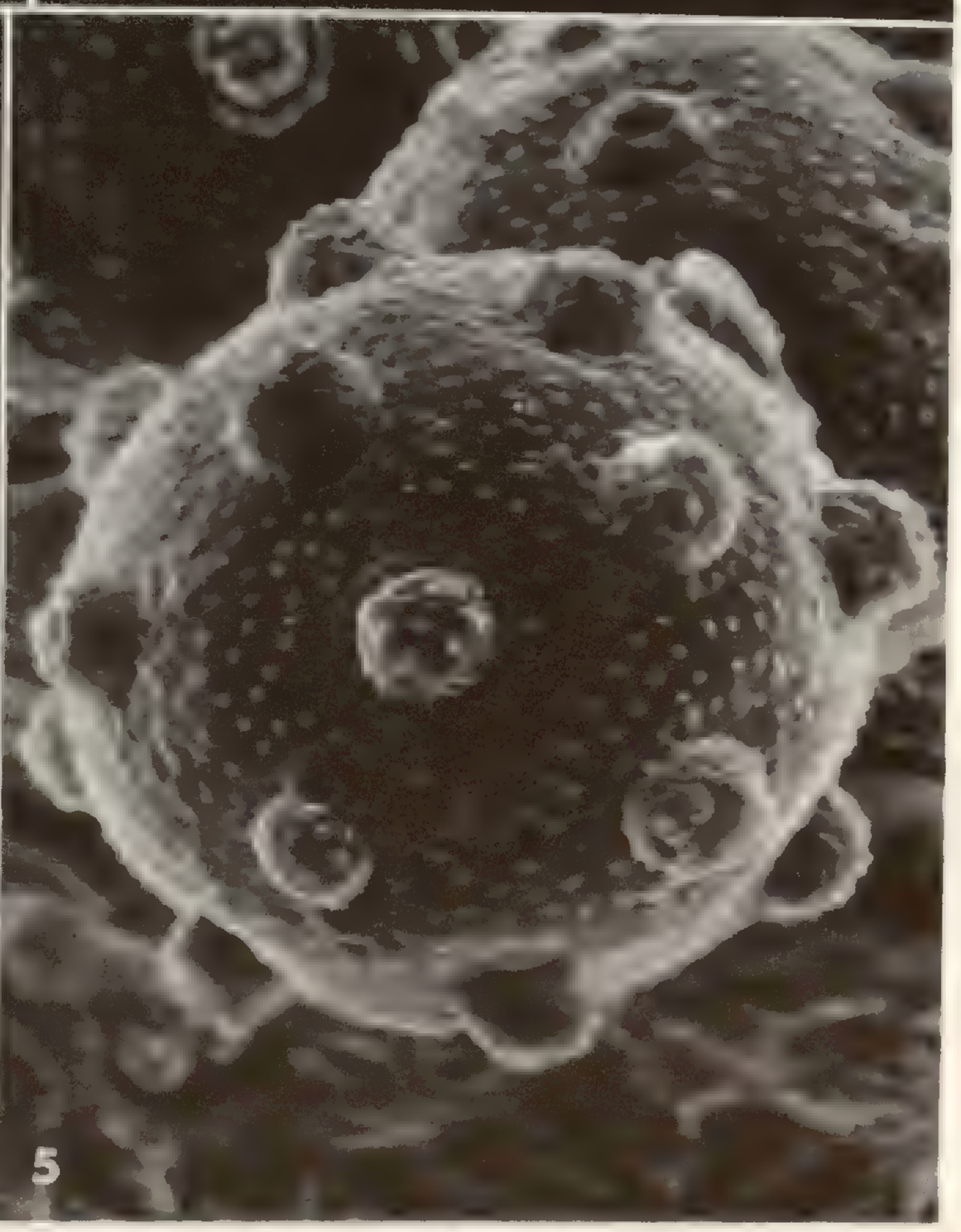
The fate of a successful pollen grain is to alight on a suitable receptive stigma. The receptive surfaces of stigmas are found in many structural and physiological states (Y. Heslop-Harrison & Shivanna, 1977), but all must provide the conditions for rehydration of compatible pollen as an essential preliminary to germination.

Rehydration reverses the changes that occur during the final period in the anther, but we can say a good deal more about the details because the events can be observed much more readily.

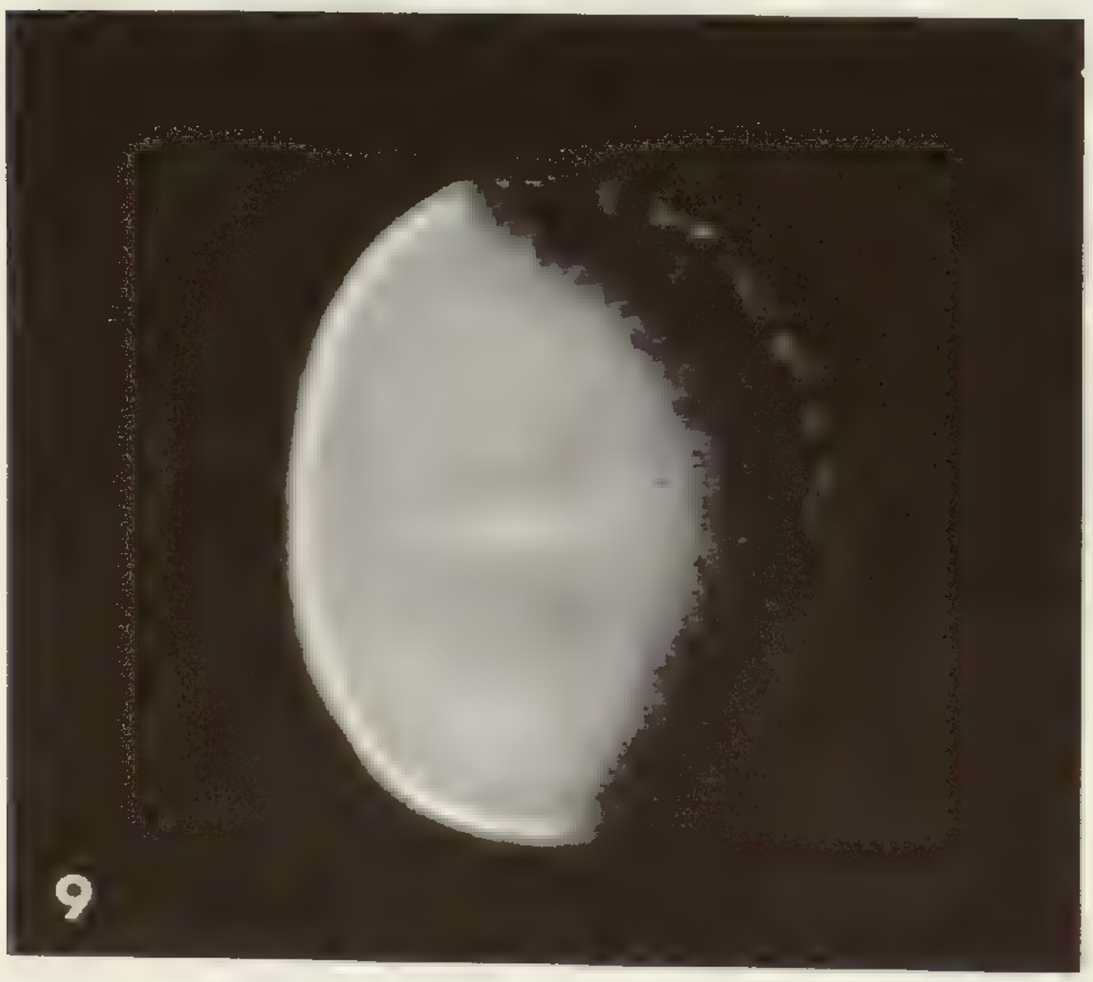
The time course of rehydration preparatory to germination is shown for three species with different intine types in Fig. 1. These measurements were made directly on the stigma using time lapse photography. All of the species have "dry" stigmas (Y. Heslop-Harrison & Shivanna, 1977), so that the grains abstract

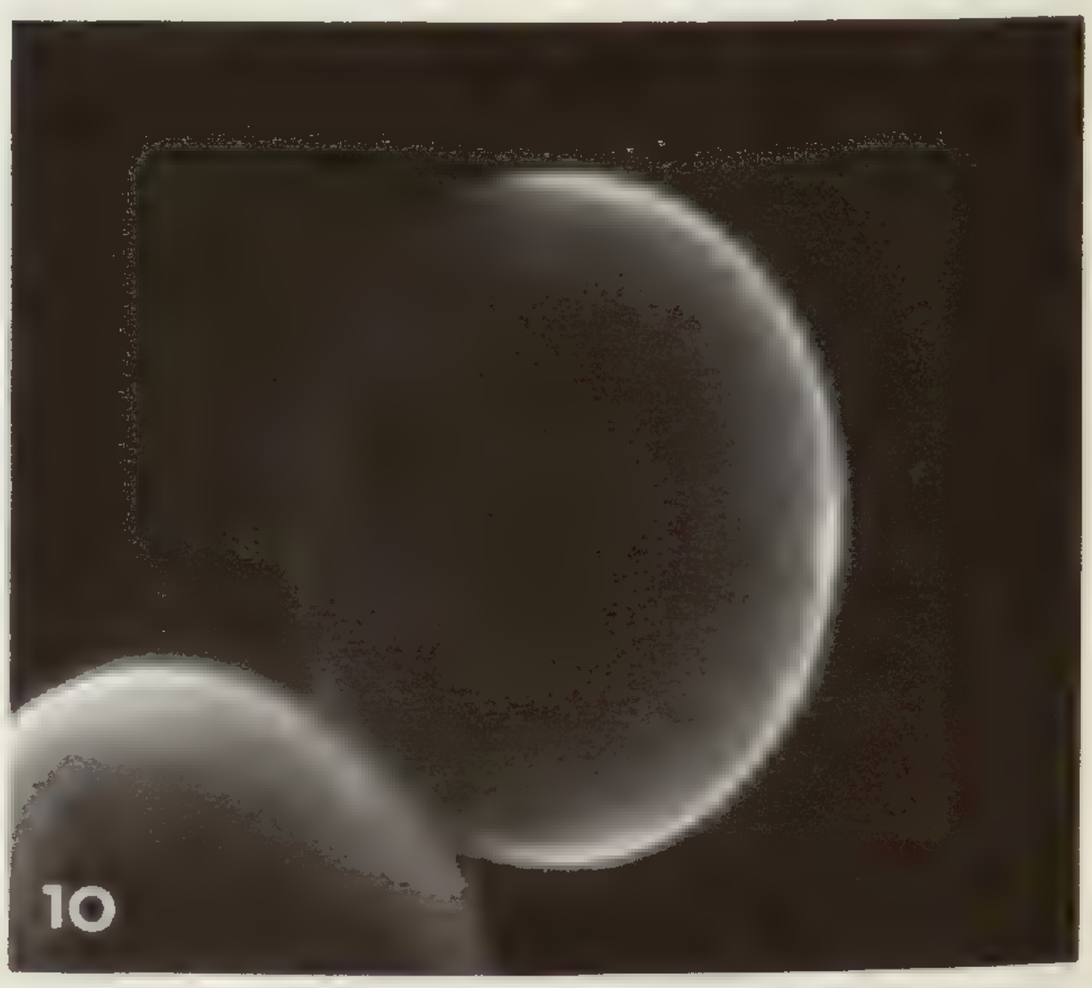


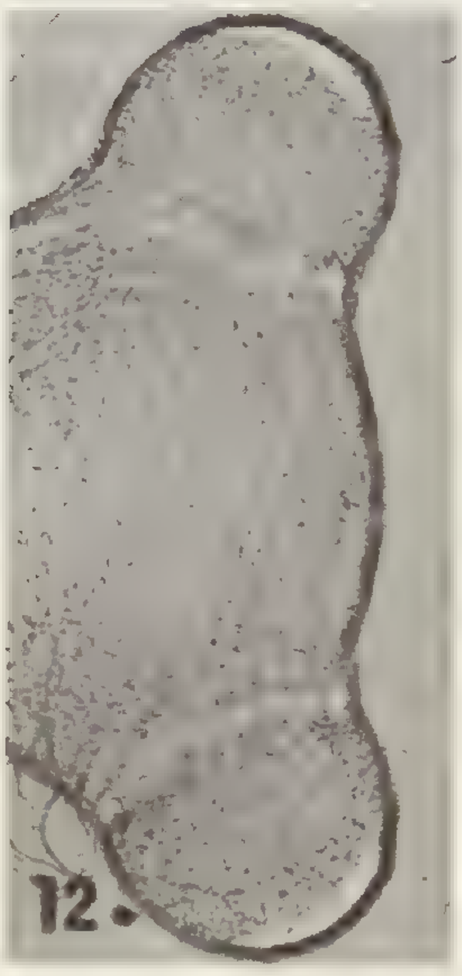


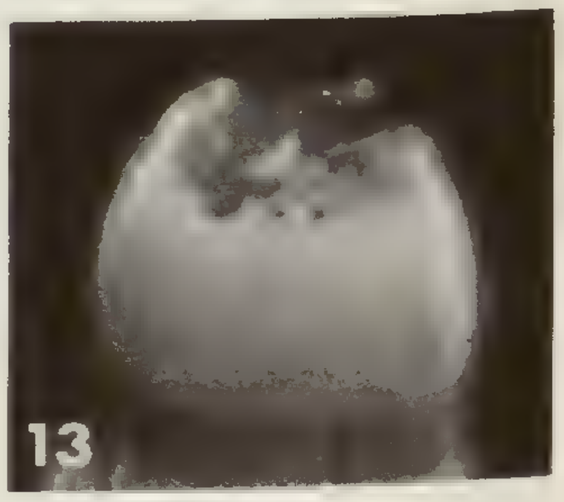


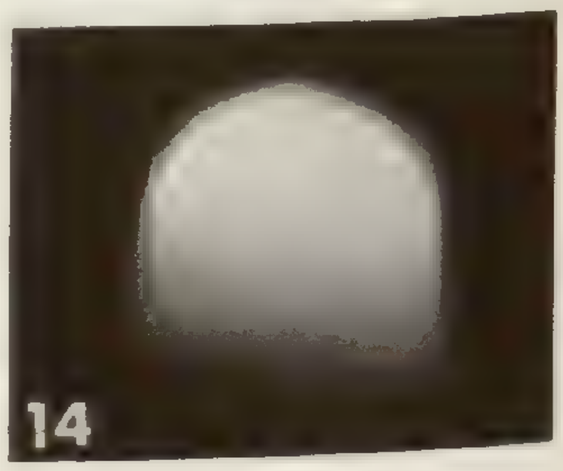
FIGURES 2–5.—2. Pollen grain of *Agrostemma githago* (Caryophyllaceae) suspended in a polyethylene glycol solution of an osmotic pressure of 5.7–6.0 MPa. The arrow shows an operculum, pressed into the surrounding sporopollenin annulus and so offering an effective seal; ×650.—3. As Fig. 2, grain suspended in a medium that allows some expansion of the grain. The arrow points to an operculum which is now rising slightly under the pressure of the underlying intine; ×650.—4. Grain in a germination medium that allows normal hydration. An operculum has lifted (arrow), and the pollen tube (T) has emerged; ×650.—5. Scanning electron micrograph of a pollen grain of *Agrostemma githago* in a state of full imbibition, showing the elevated opercula and exposed exines at each apertural site; ×700.











FIGURES 6–14.—6. Pollen grain of *Iris* (Iridaceae) suspended in a polyethylene glycol solution of an osmotic pressure of ca. 5.5 MPa. The grain has scarcely enlarged, and the lipid seal still lies over the colpus (L); ×425.—7. As Fig. 6, grain in a medium that allows some hydration. The lipid over the colpus is beginning to disperse; ×425.—8. Grain in a germination medium that allows normal hydration; ×425.—9. As Fig. 8, fluorescence micrograph after auramine O staining to reveal the

all of the water from the contiguous stigma papilla. The hydration and germination rates differ considerably among the three. Maximum grain volume was attained in 2–3 min in *Secale cereale*, but not until 35 min in *Crocus chrysanthus*. In each species, the attainment of full volume was followed by some shrinkage as the pollen tube emerged. In the case of *Silene vulgaris*, the grain was oriented so as to appose a germination aperture directly to the stigma surface. Grains oriented differently do not hydrate so rapidly (Heslop-Harrison et al., 1975). Orientation on the stigma is less important for the pollen grains of grasses; although there is only one germination aperture, both layers of the exine are penetrated by channels through which hydration takes place.

The ingress of water and the consequent dilation of the grain results in changes in the shape and area of the apertures. The events accompanying the dehydration before and during dispersal are, in fact, repeated in reverse. They can be followed on the actual stigma surface, or rather more conveniently on "artificial" stigmas, for example on membranes floating on germination medium, or in some instances actually in the liquid medium.

We may take as an example the pollen of *Agrostemma githago* (Caryophyllaceae). The grain freshly shed from the anther undergoes no volume changes in a solution of polyethylene glycol of a molecular weight of 400 daltons adjusted to have an osmotic pressure of 5.7–6.0 MPa. At this stage, the opercula are fitted closely into the apertures, which are somewhat depressed marginally so that the grain is at minimum volume (Fig. 2). In solutions of lower tonicity, the grain expands, and the opercula are lifted, so exposing more of the intine (Fig. 3); finally, after full hydration the intine is pushed out at each apertural site (Fig. 5), and this is the prelude to germination (Fig. 4). In *Agrostemma*, only small amounts of lipidic material are transferred from the tapetum to the exine during the maturation of the pollen, and these are dispersed early during hydration, rapidly exposing the apertural intine.

Obviously, the implication of these changes is that the more the grain hydrates, the lesser the hydraulic resistance to further inflow of water. Uptake is therefore governed by a neat feedback mechanism. The sequences of Figs. 6–10, 11–14 and 15–17 illustrate how the same principles apply to colpate and tricolporate grains. In two of these examples, the colpi were initially sealed by the tapetally derived lipids. These are dispersed in the bathing medium; the colpi then progressively gape, exposing more and more of the intine until finally the exposed surface accounts for some 30% of the total area of the grain in the colpate grain of the iris and 40% of the tricolporate grain of *Tagetes*.

The pathways of water uptake during initial hydration can be identified by

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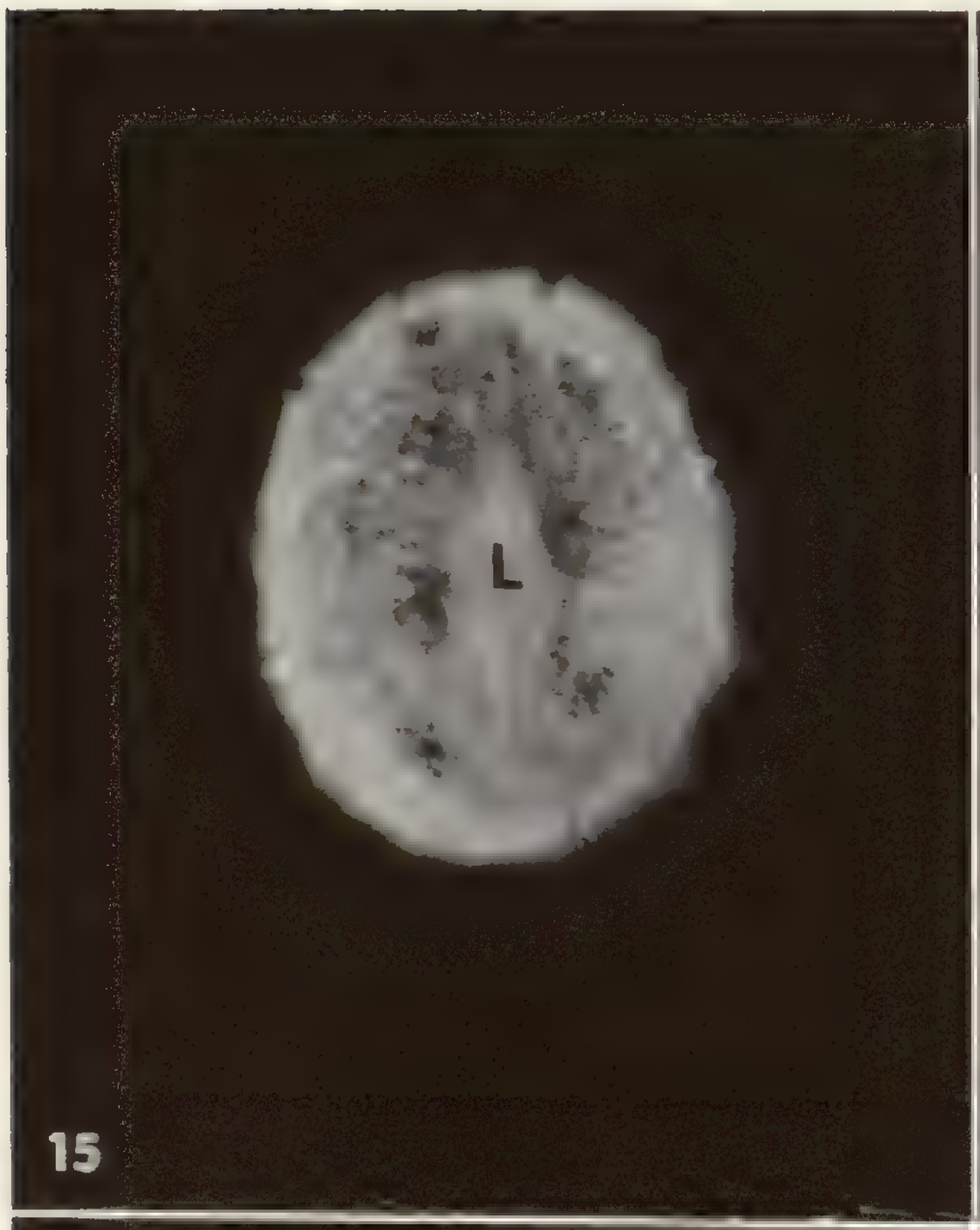
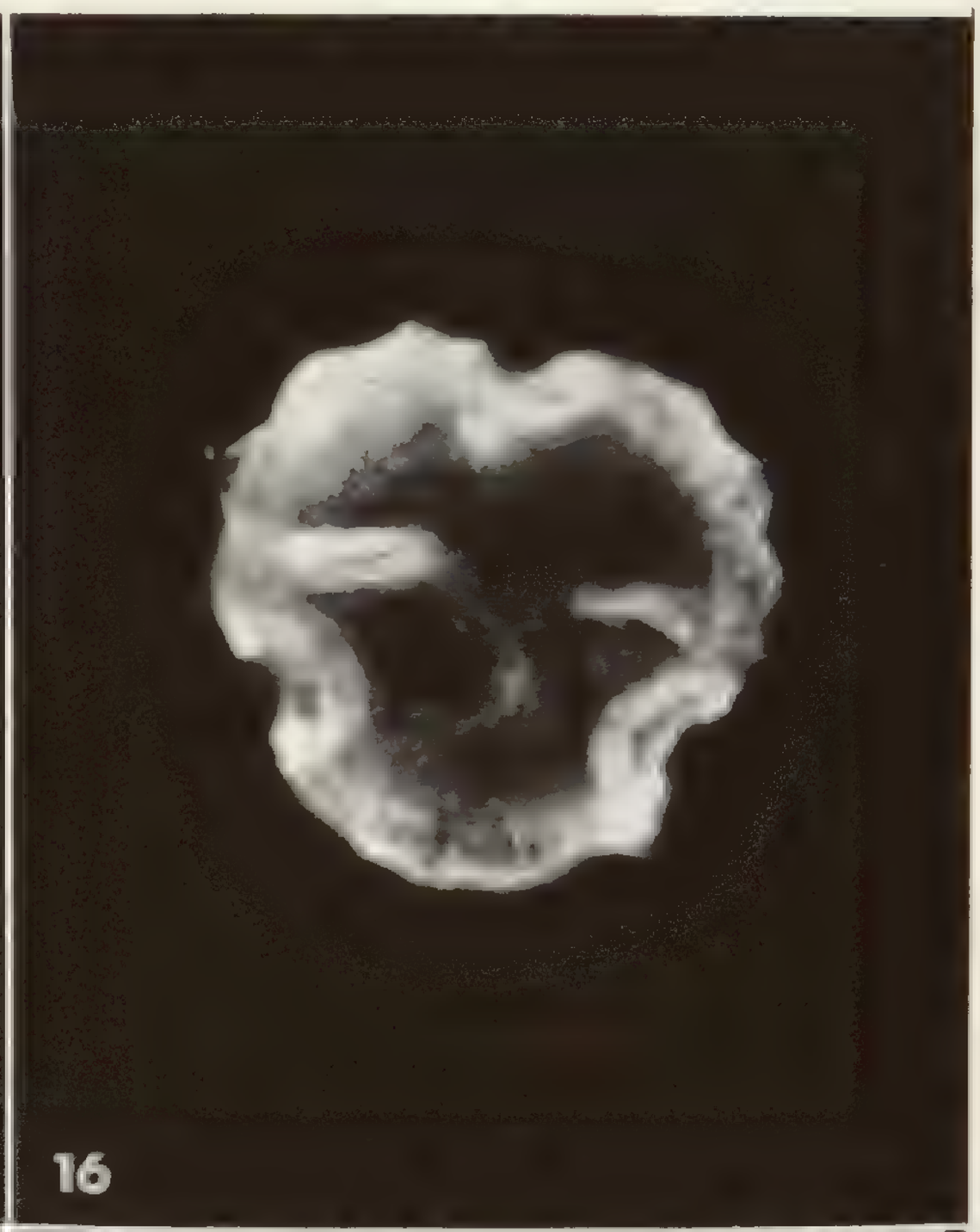
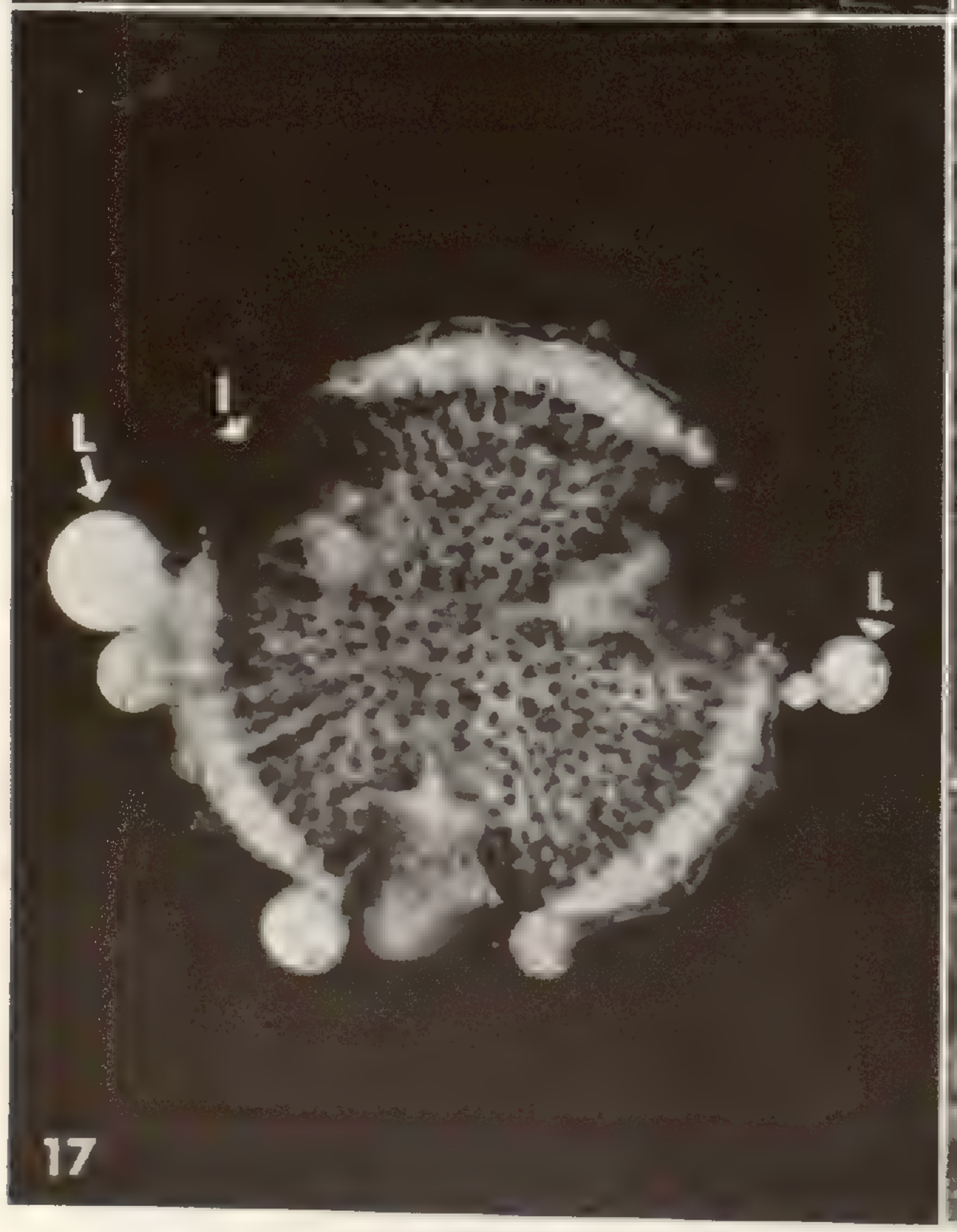
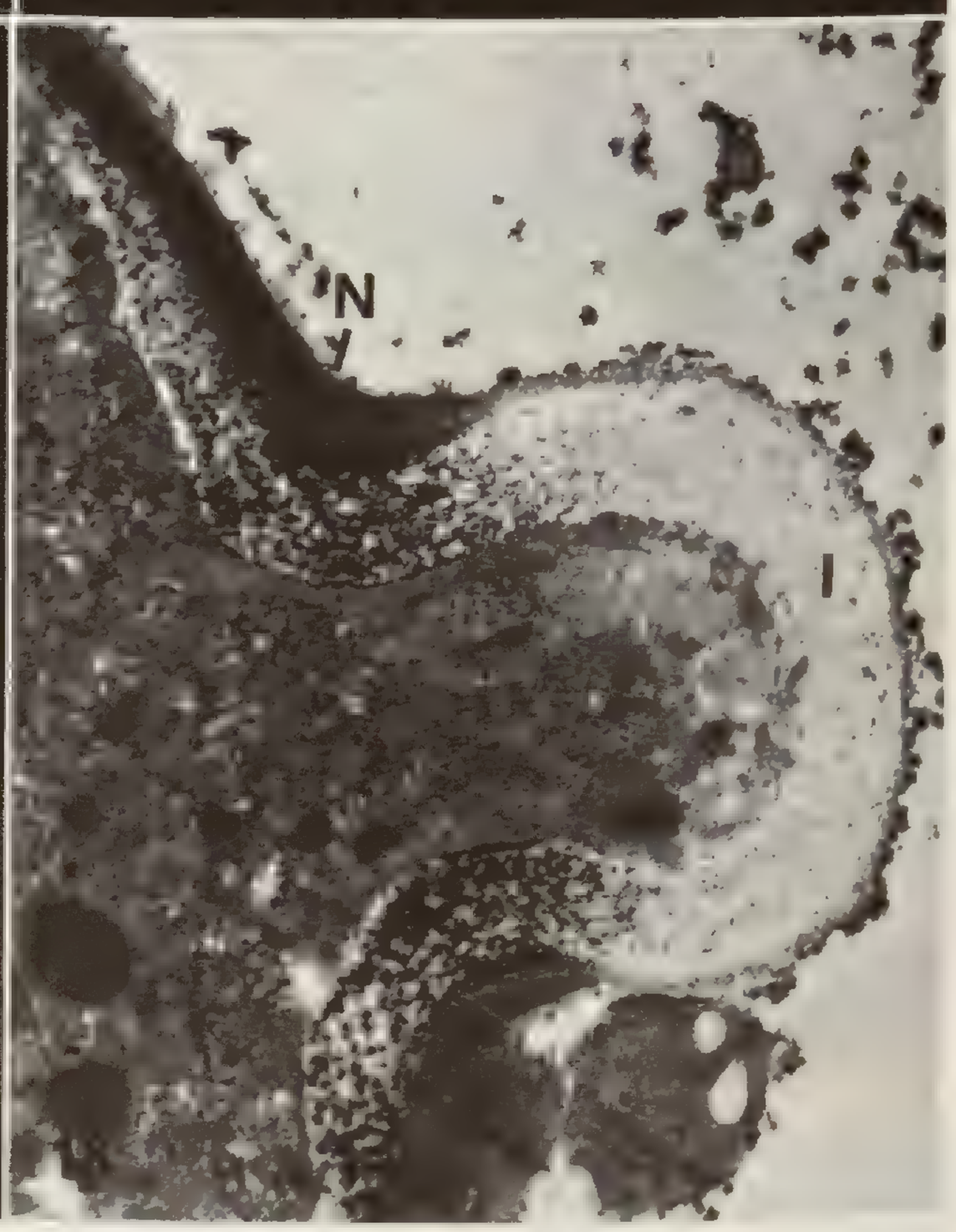
←

exine; ×400.—10. As Fig. 8, fluorescence micrograph after calcofluor white staining to reveal the apertural intine, now fully exposed; ×400.—11. Pollen grain of *Oenothera organensis* suspended in a polyethylene glycol solution of osmotic pressure ca. 6.0 MPa. The exine is infolded at each apertural site. The seal in this case is given by numerous interlocking sporopollenin lamellae in the throat of each aperture; little surface lipid is present; ×300.—12. As Fig. 11, grain suspended in a germination medium. The intine at the apertural sites is now everted, and the sporopollenin plates are torn apart; ×300.—13. As Fig. 12, auramine O staining to show the torn exine; ×350.—14. As Fig. 11, calcofluor white staining to show emergent intine; ×350.









FIGURES 15–18.—15. Pollen grain of *Tagetes patula* (Compositae), suspended in a solution of polyethylene glycol with an osmotic pressure of ca. 6.0 MPa. The grain has undergone no expansion, and the three colpi are still closed and sealed by lipid (L); ×800.—16. As Fig. 15, polar view showing the three colpi; ×800.—17. Pollen grain of *Tagetes patula* in a medium allowing normal hydration. The aperture sites are now gaping, and the underlying intine (I) is revealed. The lipids (L) are dispersing into the medium; ×800.—18. Electron micrograph of an aperture of a pollen grain of *Cosmos bipinnatus* (Compositae), after hydration in a medium containing the electron-opaque tracer, colloidal lanthanum nitrate. The intine (I) has emerged from the aperture as it would in a normal germination. The tracer has, however, entered through the aperture in the early period of hydration, and is present underneath the adjoining nexine (N). The nexine is itself impermeable to the tracer. The presence of the tracer inside the protoplast of the vegetative cell suggests that the plasmalemma does not form an effective barrier during the early stages of hydration; ×4,500.

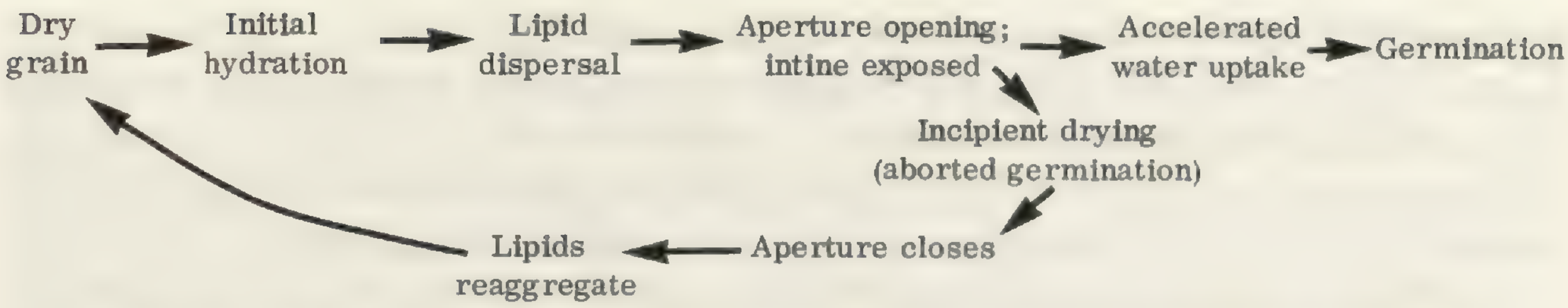


FIGURE 19. Normal sequence of hydration in pollen grains up to the point of germination.

following the movement of suitable electron-opaque tracers. Figure 18 shows the distribution of colloidal lanthanum nitrate supplied to the pollen of *Cosmos bipinnatus* at the time of first exposure to the hydrating medium. The tracer moves into the sexine and cavea, but does not penetrate the nexine, which is without channels in this species. The principal passage into the grain, however, is through the aperture sites. The tracer passes freely into the intine, and is dispersed tangentially through it under the nexine neighboring the apertures, as well as moving into the vicinity of the plasmalemma.

An important feature of most of the more elaborate apertural regulating mechanisms, and one of undoubted adaptive value, is that their function is reversible almost up to the point where the grain actually germinates. This can be demonstrated very readily using artificial stigmas consisting of thin gel layers. On these, the pollen grains can be taken through successive cycles of low and high atmospheric humidity. Viability is progressively lost, but many species survive two or three such cycles.

The normal sequence of hydration up to the point of germination is summarized in Fig. 19, which also shows how, up to a certain point in the time before the actual emergence of the tube, the sequence may be reversed. Figure 19 takes no account of the exudation phase which, as we shall shortly see, may be interpolated early in the period of hydration.

REGULATORY FUNCTIONS OF THE STIGMA

The source of the water entering the pollen is of course the stigma. As we have already noted, the receptive surfaces of angiosperm stigmas are highly diverse, but a broad division may be made into those which bear a free fluid surface at maturity ("wet" stigmas) and those without a free-flowing secretion pool ("dry" stigmas). While in the receptive state stigmas are more or less freely exposed to the atmosphere, so all must be subject to considerable evaporation. As yet we are without data for the evaporative loss from wet stigmas, but this might be expected to vary considerably according to the effectiveness of lipid coatings (Konar & Linskens, 1966) and to the concentration of osmoticum in the secretion.

Dry stigmas have the capacity for regulating water loss through the surface of the papillae by varying the hydraulic resistance of the cuticle (Heslop-Harrison, et al., 1975; Heslop-Harrison, Heslop-Harrison & Barber, 1975). The stigma papilla is a secretory epidermal cell with a pectocellulosic wall limited by a cuticle, but the cuticle, being made up of radially oriented cuticularized rods or columns, is always discontinuous. In the turgid papilla, the rods are drawn apart on the surface

of the expanded wall, allowing free passage of water. With the loss of turgidity the papilla shrinks and the cutinized rods are brought into closer contact, with a consequent restriction of the pathways available for water movement.

The stigma has thus the capacity for regulating water flow, just as the pollen has, and it will be seen that the system allows for adjustment to a wide variety of circumstances (Heslop-Harrison, 1979). It conserves the capacity of the pollen grain to resist excessive desiccation right up to the moment when circumstances are propitious for germination and the entry of the tube. For example, a plant in a state of water stress may receive pollen, but will be unable to provide the conditions for hydration until an appropriate water balance has been achieved in the stigma. At this point the pollen will be permitted to begin hydration, and at an increasing rate, as long as the water flux from the stigma continues. Should the flow be inadequate to support full hydration, the sequence will reverse, the grain will begin to dry out and the apertures will close once more. Such an episode need not necessarily affect the possibility of future success when the water balance of the stigma is restored.

MEMBRANE PERMEABILITY, DESICCATION AND HYDRATION

With a few rare exceptions, viable angiosperm pollen grains lack vacuoles at the time of dispersal. This implies that the water potential of the grain is likely at first to be established by the matric potential attributable to the colloids of the protoplast and wall and the solutes present in the cytoplasm of the vegetative cell. In the desiccated grain, a cell "membrane" as such is unlikely to exist, the membrane lipids being distributed in micelles in the condition of minimal water content—comparable, that is, with the membranes of desiccated seeds (Heslop-Harrison, 1979). In the system overall, the only effective semipermeable membranes will thus be those of the stigma papilla.

After hydration has begun, however, the membranes are quickly reorganized in the pollen grain. In rye, this can take place in two to three minutes, at which time the first movements of the protoplasm can be seen in the grain. Vacuolation occurs in under 5 min in rye, and by this time germination will normally have begun, and normal tonoplast, plasmalemma, and endoplasmic membranes can be seen with the electron microscope. The periods are undoubtedly longer for other species (Fig. 1), but the sequence of events is always the same in those pollens that are dispersed in a partly dehydrated state. The later growth of the tube and the transfer of cytoplasm and reserves from the grain into it is accompanied by the enlargement of the vacuolar system, and this must also be supported by transfer of water from the stigma until such a time as the pollen tube has entered the transmitting tract.

The water potential of the grain when first in contact with the stigma will be influenced not only by osmotic forces but by pressures attributable to the wall. In the dehydrated grain at minimum volume the wall will apply a tension to the protoplast of the vegetative cell. During the rehydration of the grain, a point will be reached when the wall exerts no pressure, and with further inflow of water the pressure will become positive. While the membranes of the vegetative cell remain ineffective as osmotic barriers, this pressure will be exerted only on the protoplast, in effect balancing matric potential. Further passage of water will

continue, however, while the water potential of the grain remains lower than that of the stigma papilla in consequence of the solutes of the pollen, and this must lead to exudation.

The transition to this phase is seen spectacularly in the grasses, an observation first made by Watanabe (1955). Exudation is first seen from the germination aperture, and then through the micropores of the exine. In rye the outflow may account for as much as 15% of the volume of the grain.

When the membranes of the pollen grain have become reorganized, the vegetative cell begins to act like any somatic cell of the plant, and the familiar laws governing plant-cell water relations begin to apply. Containment of the solutes in a semipermeable membrane restricts their movement into and through the wall, and further endosmosis will be exclusively *into* the grain. Exudation will then cease, and further expansion will begin; but in the normal course of events this will mark the moment of germination, and enlargement in volume will be in consequence of the growth of the tube.

Apertural Mechanisms and the Function of the Wall as a Repository

In many angiosperm families the pollen wall conveys enzymes and other proteins (for reviews of this function, see Heslop-Harrison, 1975a, 1975b). The protein load of the *exine*, like its surface materials, is derived from the tapetum of the anther, and that held in the *intine* is inserted during the thickening of this layer of the wall in the spore and young pollen grain, the source being the male gametophyte itself. In aperturate grains, the exine materials are held in the cavities and sculpturings of the sexine in the nonapertural areas, while the intine protein load is concentrated in the region of the apertures (Heslop-Harrison, et al., 1973).

In families with aperturate grains and exine storage—such, for example, as the Cruciferae and Compositae—proteins from the exine domain are released very soon after the beginning of hydration, passing out onto the stigma surface and associating there with materials from the stigma cells, while the intine proteins are released only after the grain has become partly hydrated (see, for example, Howlett, et al., 1973).

Consideration of the sequence of events accompanying the initial hydration shows why this should be so. At first, the net flux of water will be *into* the grain at the apertural sites as the intine is progressively exposed. As full turgidity is approached, the tide will be turned; the phase of exudation follows, and for a while the net flux is outwards from the grain. At this time mobile fractions held in the apertural intine will be flushed out onto the stigma surface.

Apertural mechanisms thus play a part in regulating the outflow of intine-held proteins. There seems to be something of a compromise, here, however, for such devices could act to prevent premature release only in the first period of hydration; once the phase of exudation is reached one might expect mobile constituents of the intine to be lost irrevocably. The functions of the enzymic load of the apertural intine are still to be fully explained, but two roles are attributable to them, (a) in the softening of the intine at the germination site, as essential prelude to the emergence of the tube tip (Stanley & Linskens, 1974; Konar & Stanley,

1969), and (b) in the early interactions with the stigma, most probably during the penetration of the cuticle and perhaps in the early nutrition of the pollen tube (Heslop-Harrison, 1971). A further possibility is that the intines of certain species carry proteins concerned with the recognition reaction of gametophytic incompatibility systems (Heslop-Harrison, 1978), but in no case has this been shown experimentally as yet.

In certain advanced pollen types, the germination apertures are equipped with devices facilitating the penetration of the exine and the emergence of the tube tip. In the grasses and various other families with operculate apertures, the first stage of germination involves the Zwischenkörper, an outer layer of the intine, composed of pectic substances, underlying the operculum at the aperture. With the beginning of hydration, the Zwischenkörper swells to form a gel, and it is this gel that first lifts the operculum. The emerging tube tip pushes through the gel, which is then dispersed. Germination is prevented if the calcium ion concentration of the medium is raised beyond the optimum, apparently through the rigidification of the pectins of the Zwischenkörper. The same result is obtained if an appreciable proportion of the intine protein is leached out in a medium of suitable tonicity before the conditions for germination are offered. In each case the grain is "switched on" metabolically speaking, but fails to produce a tube. That the treatments are in no sense lethal to the protoplast is shown by the persistence of cytoplasmic streaming and the progressive digestion of storage starch.

Presumably the intine enzymes are involved both in the dispersal of the Zwischenkörper and in the early relaxation of the underlying cellulosic part of the wall essential for the formation of the tube tip. Their loss therefore blocks germination. From these experiments with grass pollens one may deduce the reason for the fact that, in general, pollens lose viability on leaching even when they survive the treatment in a structurally intact state.

WHY SEVERAL APERTURES?

Monocotyledons characteristically have a single germination site, and most dicotyledons have three; but trends towards higher numbers have seemingly arisen several times in the evolution of flowering plants. Presumably some functional significance attaches to this.

Certain correlations can be suggested. Although adequate statistical data are not available, I suspect that it would turn out that the ratio of apertural area, measured as mean area of aperture × mean number per grain, to total wall area would vary less among and within the various groups than pollen grain size itself, certainly among species with dry stigmas; and it might even emerge that larger grains have proportionately greater apertural areas through which intine contact might be made. The rationale of this is simply that, wherever hydration depends upon the establishment of continuous water films between the apertural intine and a dry stigma surface, selection might be expected to favor a geometry that would optimize the chance of direct contact between the aperture and the porous cuticle of the papilla.

Aperture shape becomes a factor here, and also the porosity of the exine. Only some 0.4% of the large pollen grains of *Zea mays* might, on statistical grounds, be expected to hydrate at all from the stigma were the only pathway of

water uptake the single aperture; as it is, most grains hydrate through the micropores of the exine. In contrast, the equally large pollen grains of certain Malvaceae have a thick nexine, unperforated by micropores. Compensation is here offered by the presence of numerous apertures, and sometimes also by another intriguing adaptation, this time on the part of the stigma papillae, which often embrace the grains after capture, so bringing the porous papillar cuticle into contact with several apertures.

Stigmas of the dry type do offer rather difficult conditions for pollen hydration, and adjustment to these must obviously require specialization of the exine and the apertural mechanisms. The evolution of forate exines, with several more or less circular apertures, seems to be one of these specializations. I am aware of no exceptions to the rule that forate exines are associated with dry stigmas; and this certainly seems to imply a physiological correlation. The clue is given by the behavior of pollens like those of the Caryophyllaceae on the stigma (Heslop-Harrison et al., 1975). The apertures closest to the stigma surface form the first routes for the ingress of water, and the intine underlying these apertures is thus the first to become hydrated. Presumably, enzymic softening of the intine begins rather earlier at these sites, so it is to be expected that the tube should emerge from one of them, as is generally to be observed. In the large grains of genera like *Hibiscus* the same localization of emission and tube outgrowth can be seen, and the Malvaceae also offer spectacular examples of polysiphonious germination where tubes emerge from several of the apertures adjacent to the contact face with the stigma.

The adaptive value of the forate exine therefore probably lies in the way it allows for the highly localized activation of apertural intine sites. The adaptation would clearly have no value on a wet stigma where hydration and germination occur while the grain is wholly or partly immersed in the stigma secretions.

Anomalous Pollen Types and the Transfer of Function

In my introductory remarks I referred to the likelihood that the diversity of pollen walls would not only reflect the multiplicity of selective pressures to which the various functions have been exposed in the course of angiosperm evolution, but also the fact that the same functional end may well be attained by different means. It is an enlightening exercise to compare different taxonomic alliances with these points in mind. There are clearly certain irreducible functions, such for example as those concerned with hydration, tube emergence, and stigma penetration. There are others that are of the nature of options. To take one instance: in some families, as we have seen, the exine is the repository for a substantial load of sporophytically synthesized materials, which apparently have functions in the interaction with the stigma; yet in other families, the exine carries little or no tapetal material.

This reduction in the function of the exine is strikingly obvious in certain groups. The baculate type of exine has been lost from various modern angiosperms, apparently by secondary simplification (Nilsson & Skvarla, 1969), and this must of course have meant the sacrifice of the capacity to convey sporophytic surface materials in exine cavities. A sequence can be traced in the group of monocotyledonous families constituting Engler's Scitamineae, including Musa-

ceae, Strelitziaceae, Heliconiaceae, Marantaceae, Cannaceae, and Zingiberaceae (Heslop-Harrison, 1976). In some representatives, an exine is present with a rudimentary baculate system; in others it forms no more than a single thin layer without included cavities and in still others (e.g., *Canna,* Skvarla & Rowley, 1970) it is reduced to isolated papillae overlying a thick intine. This sequence can be connected through various Liliiflorae such as *Crocus* and *Sternbergia* to genera in which the baculate exine is fully developed. Intriguingly, this regression of the exine is accompanied by an elaboration of the intine. The intine is generally thicker in the genera with reduced exines, and the system of internal inclusions is better developed, in the extreme examples extending over the whole surface of the grain, as first reported by Skvarla & Rowley (1970). These inclusions are derived from microvilluslike extensions of the membrane of the vegetative cell which are cut off into the intine as it thickens, and each is a repository of a range of hydrolytic enzymes similar to those found at the apertural sites of aperturate pollens (Heslop-Harrison, 1975b, Y. Heslop-Harrison, 1977). In some sense, therefore, we see a function of the exine transferred to the intine; but the detailed physiological relationships remain to be worked out. It would, for example, be profitable now to compare the water economy of the pollens of *Lilium* and the exineless Scitamineae. The absence of the protecting exine in the latter must have some consequence; but I suspect it might prove that a full understanding of the situation would require that the pollination biology be taken into account, and especially the conditions of dispersal in the natural habitat.

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POLLEN LOADS OF HONEY POSSUMS (*TARSIPES SPENSERAE*) AND NONFLYING MAMMAL POLLINATION IN SOUTHWESTERN AUSTRALIA[1]

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ABSTRACT

Pollen loads were analyzed from 30 honey possums in the Albany region of southwestern Australia. The pollen of *Banksia attenuata* was the major component of the pollen loads followed by *Adenanthos cuneata* and *Banksia coccinea*. The data from pollen loads and flower-head morphometrics indicate that *Tarsipes* is the primary pollinator of *Banksia attenuata*, and not birds as might be surmised from other characteristics. *Tarsipes* also visits typically bird-pollinated plants such as *Banksia coccinea* and *Adenanthos cuneata*, but little or no pollination would be expected from such visitation. The lack of distinct flowering seasonality in the southwestern Australian flora is correlated with the presence of a high percentage of long-lived, resident pollinators such as birds and nonflying mammals. A number of plant genera are mentioned which show possible adaptations for pollination by nonflying mammals. Several groups of small mammals which might play a role in pollination are also discussed.

Pollination by nonflying mammals has been the subject of renewed interest in recent years (Rourke & Wiens, 1977; Wiens & Rourke, 1978; Sussman & Raven, 1978; Holm, 1978; Carpenter, 1978; Hopper, unpubl. man.). There is, however, a dearth of definitive and, especially, quantitative data on the subject. Any general analysis of pollination by nonflying mammals must consider the unusual biota of southwestern Australia. This region has the highest concentration of plants presumed to be pollinated by these animals. One of the most unusual mammals in southwestern Australia (if not the world!) is the mouselike marsupial honey possum (*Tarsipes spenserae*). The incredible adaptations of this animal to a presumed diet of nectar (and pollen?) were summarized by Rourke & Wiens (1977) and Holm (1978). Various aspects of its biology were discussed by Vose (1972, 1973) from observations on animals in captivity. It is widely assumed, especially by Australian biologists, that the honey possum is a coadapted pollinator of various plants in the region, but we are unaware of any published information to corroborate these assumptions. The primary object of the study, therefore, was to determine if captured feral honey possums carried pollen loads, and if such pollen is positioned to effect regular pollination of those flowers involved.

METHODS

Honey possums and meliphagid birds (honey eaters) were captured during three successive days and nights (Dec. 1–3, 1978) at two study sites (Umagallee and Kaylah) on the William Dunlop farm along Highway 1, approximately 45

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km east of Albany, Western Australia. The vegetation of this area is composed of dense sclerophyllous shrubs often dominated by *Banksia* (and the ubiquitous Australian flies!). Locally the area is known as heathland or quangen and is part of the southwestern floral province of Australia, which is characterized by an exceptionally high diversity of species.

Honey possums were live-trapped in pits 40–50 cm deep. The pits were lined with smooth plastic drainpipe (7.5 cm in diameter) to prevent trapped animals from escaping up the sides. The traps were checked early each morning and the captured animals tested for pollen on the snout and forehead and released. Honey eaters were trapped in mist nets, checked for pollen, and also released.

The presence of pollen was determined by rubbing gelatin blocks approximately 5 mm^2 and 2 mm thick through the hair or feathers of the respective animal (Beattie, 1971). The blocks were then placed on a warmed slide, melted, and spread under a cover glass 22 mm^2. Such slides are prepared in seconds and the pollen adhering to the blocks is readily trapped and stained (basic fuchsin is a component). When cooled, the preparation is essentially permanent. Identification of the pollen, where possible, was accomplished by comparison to samples taken from flowers collected on the study sites.

Freshly defecated feces were obtained from two newly captured *Tarsipes* and similarly sampled for pollen content, except that the gelatin block was simply touched directly to the surface of the soft fecal mass. The number of pollen grains on the slides was determined by systematic scanning of the gelatin layer under a compound microscope. In fecal samples, however, the pollen grains could not be counted precisely because of the large numbers involved.

Results

Thirty honey possums were captured during the study. All carried pollen on their snout and forehead, however, the quantity varied widely (Table 1). The pollen loads were derived from at least 12 species of flowering plants, but the pollen of *Banksia attenuata* was clearly the most common. The high number of *Adenanthos cuneata* grains was due primarily to a single sample (No. 10) which accounted for 536 of the 854 total and distorted both the total and the mean for this species. A more accurate indication of the importance of this species in terms of pollen load composition is evident from the mode, which is approximately four times higher for *B. attenuata*. The pollen of *Callistemon speciosus* and *Banksia coccinea* was present in approximately equal proportions. The remaining pollen represents a number of unidentified species not observed in the immediate areas of the study sites.

Only three species of flower birds (Meliphagidae) were captured, but their pollen loads were much larger than on *Tarsipes*. Presumably this is because *Tarsipes* frequently removes pollen by grooming (Vose, 1972). Birds may occasionally preen themselves, but they were effectively immobilized in the mist nets whereas the honey possums captured in pit traps had freedom of movement for grooming. Also the pollen loads on the honey eaters was much less diverse and composed almost entirely of pollen from *Banksia coccinea* and *Adenanthos cuneata*; no pollen of *B. attenuata* was present.

The fecal samples of *Tarsipes* were of special interest because they were

TABLE 1. Pollen loads of *Tarsipes spenserae* and Meliphagidae from southwestern Australia.

Animal	Sample No.	No. of Pollen Grains											
		Banksia attenuata	*Banksia coccinea*	*Banksia grandis*	*Adenanthos cuneata*	*Callistemon speciosa*	*Hakea sp.*	*Melaleuca thymoides*	*Petrophile longiflora*	Sp. A.	Sp. B.	Sp. C.	Sp. D.
Tarsipes spenserae	1	4	2		2								
Tarsipes spenserae	2	3			1					125		1	
Tarsipes spenserae	3	17	1							5			
Tarsipes spenserae	4	6			12					2			
Tarsipes spenserae	5	10	12		13					1			
Tarsipes spenserae	6	51	1		27					1			
Tarsipes spenserae	7	113	2		10						24		
Tarsipes spenserae	8	35	1		1						3		
Tarsipes spenserae	9	6	31		28				3		7		
Tarsipes spenserae	10		87		549	1						1	
Tarsipes spenserae	11	15		3	23								
Tarsipes spenserae	12	7			3								
Tarsipes spenserae	13				2								
Tarsipes spenserae	14	1	12		1					153			
Tarsipes spenserae	15	115		1	3	1				27			
Tarsipes spenserae	16	36	6		7								
Tarsipes spenserae	17	66											
Tarsipes spenserae	18	46	2		42	1							
Tarsipes spenserae	19	3											
Tarsipes spenserae	20	35			5	2				3			
Tarsipes spenserae	21	6	1			3							
Tarsipes spenserae	22				2	2							
Tarsipes spenserae	23	40			2	2							
Tarsipes spenserae	24	11	1			4				1			
Tarsipes spenserae	25	1	2		25								
Tarsipes spenserae	26	106	2	2	2								

TABLE 1. Continued.

Animal	Sample No.	No. of Pollen Grains											
		Banksia attenuata	*Banksia coccinea*	*Banksia grandis*	*Adenanthos cuneata*	*Callistemon speciosa*	*Hakea sp.*	*Melaleuca thymoides*	*Petrophile longiflora*	Sp. A.	Sp. B.	Sp. C.	Sp. D.
Tarsipes spenserae	27	149	9	5	53								
Tarsipes spenserae	28	1			22								
Tarsipes spenserae	29	53	4		2								
Tarsipes spenserae	30	38	3		4								
Total		974	191	11	854	19			3	318	34	2	
Mean		32	6	0.4	28	0.6			0.1	11	1	0.06	
Mode		11	1	0	3	0			0	0	0	0	
Acanthorhynchus superciliosus[a]	1				100%								
Acanthorhynchus superciliosus[a]	2		<0.01%		73%		<0.01%	<0.01%					26%
Phylidonyris novae hollandiae[a]	3		71%		29%								
Phylidonyris novae hollandiae[a]	4		83%		17%								
Phylidonyris nigra[a]	5		75%		25%								
Phylidonyris nigra[a]	6		62%		33%		0.02%	0.03%					

[a] Because of the excessively large number of pollen grains in most of the honey eater samples (well into the thousands), all the grains were not counted and the data are expressed as percentages.

composed of almost solid pollen residue. The freshly defecated feces are a black, "mushy," amorphous mass and in no way resemble the hard fecal pellets typical of small mammals. The pollen was interspersed in a black substance giving the feces its characteristic color, and also contained numerous unidentified opaque granules (sand grains?). Because the feces were obtained immediately upon defecation, they were presumably uncontaminated.

DISCUSSION

The high percentage of pollen from *Banksia attenuata* present in the pollen loads suggests that flowers of this plant received the highest frequency of visitation by *Tarsipes* during the study period. The high density of *B. attenuata* pollen in the feces also supports this contention. Initially, this seems surprising because *B. attenuata* is a small- to medium-sized tree (up to 14 meters) with highly visible and easily accessible terminal spikes of yellow flowers (Holliday & Watton, 1975). These characteristics strongly suggest bird pollination. Several Meliphagidae (honey eaters) are known to visit the spikes, e.g., the yellow-throated miner (Morcombe, 1968), the New Holland honey eater, western spinebill, white-cheeked honey eater, and no doubt others. The pistil of *B. attenuata*, however, is only 11 mm high and many flower birds in western Australia have bills twice that length. Thus, if birds pollinate *B. attenuata*, it must be effected largely by pollen transferred from the bill. This seems unlikely since the surface of the bill is poorly adapted to hold pollen, but pollen was observed by Burbidge et al. (1979) on the beak of a New Holland honey eater. Feathers of the head and breast are the commonly used medium for retaining and transferring pollen in typical bird-pollinated species. Such a situation is beautifully illustrated in a photo by Morcombe (1968: 38) for the yellow-throated miner. The bird is shown probing the flowers of *B. attenuata*, but the style reaches no farther than about a third of the distance up the beak.

The floral morphometrics of *Banksia attenuata* are not well adapted for pollination by birds. The head of *Tarsipes*, however, does correlate with the size and shape of the flowers, especially when one considers that its brushed tongue is extensible up to two centimeters beyond the snout (Vose, 1973). The heads of *B. attenuata* also emit a fermentedlike odor, which directly supports the idea of pollination by nonflying mammals (Rourke & Wiens, 1977). Furthermore, the odor is surprisingly similar to that described by Wiens & Rourke (1978) for South African species of *Protea* pollinated by rodents. We are unaware of any typically bird-pollinated flower which produces strong fermentedlike odors. Cursory attempts to determine the time of nectar production in *B. attenuata* were equivocal, but Morcombe (1968) reports nectar production in this species is particularly abundant at night. *Tarsipes* apparently forages nocturnally and is scansorial, which further supports nonflying mammal pollination for *B. attenuata*.

If *Banksia attenuata* is pollinated primarily by *Tarsipes*, it explains the seed-set results obtained by Whelan & Burbidge (unpublished data) using exclosure experiments to exclude birds from the spikes of *B. attenuata*, *B. menziesii*, and *B. littoralis*. Seed set occurred in both *B. attenuata* and *B. littoralis*, but not in *B. menziesii*, when the spikes were enclosed in 0.5 inch hexagonal wire mesh

designed to exclude birds. The head of *Tarsipes* is approximately 11 mm wide (N = 2 animals), and is thus able to penetrate such an exclosure. We predict that *B. menziesii* is primarily bird pollinated; thus the lack of seed set in this species could also be explained.

If *Banksia attenuata* is pollinated primarily by nonflying mammals, it raises the intriguing question of how the pollinators are attracted to the spikes which may be many meters above ground level (Holliday & Watton, 1975). Odor must be the primary cue, but its effectiveness so high above ground level seems dubious. Carpenter (1978) reports that *B. ericifolia* in eastern Australia (also a small tree) secretes nectar into longitudinal channels on the spikes which then drips to the ground and lower foliage, and in this way, presumably, attracts nonflying mammals to the plants. *Banksia attenuata,* however, possesses no such nectar channels and cursory observations showed no evidence of nectar secretion from the spikes to the ground. Several banksias, however, secrete nectar directly from the tips of the corolla. Unlike most banksias, the corollas of these species remain united except at the apex. The texture of the corolla in these instances is hard and smooth. Thus they would not be expected to retain nectar easily by surface tension. *Banksia lemmaniana* is an excellent example of this "nectar drip" attraction system. Species with similar corolla types include *B. caleyi, B. elegans, B. lindleyana,* and *B.* sp. nov. (George, pers. comm.). Keighry (pers. comm.) states that *B. tricuspis* also secretes nectar from the spikes, but utilizes a different method. Some of these species also have pendulous heads, which might be important in this particular system of "nectar drip" attraction.

Carpenter (1978) also suggested that the hooked style in some species of *Banksia* was an adaptation for pollination by nonflying mammals. This is almost certainly correct, but in addition many straight-styled species, such as *B. attenuata* and *B. lemmaniana,* are also probably pollinated by nonflying mammals. We estimate that perhaps 50% or more of the banksias are mammal pollinated.

The high concentration of pollen residue in the feces of *Tarsipes* indicates it is largely a pollen feeder, or that pollen (as in many bats) is at least an important element of the diet. Supporting this contention is the fact that in several instances captive *Tarsipes* primarily licked the pollen from the styles of *Banksia attenuata* and also probed for nectar. Vose (1972) also mentioned that captive *Tarsipes* licked pollen from the flowers. The pollen mass of *B. attenuata* is peculiarly viscous, and perhaps it is coated with a nutritionally valuable lipid layer as recently mentioned by Baker & Baker (1979).

While the pollen of *Banksia attenuata* is the primary constituent of the pollen loads of *Tarsipes,* the pollen of *Banksia coccinea* and *Adenanthos cuneata* is also consistently present (Table 1). That *Tarsipes* (or any other nonflying mammal) is an effective pollinator of these latter two species, however, is highly improbable on the basis of both morphometric and attraction criteria. The pollen loads collected from the honey eaters, however, show that *B. coccinea* and *A. cuneata* pollen predominates and that pollen of *B. attenuata* is not present (Table 1). Thus, while birds certainly visit *B. attenuata,* they may not transfer pollen easily or accumulate it in their pollen loads; however, the sample size of honey eater pollen loads in this study is small and additional data are necessary for confirmation. Possibly *Tarsipes* visits typically bird-pollinated flowers primarily

for pollen. Because some pollen of these species also accumulates on the snout and forehead, nectar probing is also indicated, since licking pollen does not normally transfer pollen to the head of *Tarsipes*. The pollen in the feces, however, probably represents the feeding activities of no more than the previous 24 hours, whereas residual pollen in low concentrations might remain on the forehead and snout for considerably longer periods in spite of repeated grooming.

Many flowers in southwestern Australia are obviously visited by both birds and nonflying mammals and determining the relative effectiveness of these potential pollinators will not always be simple. The problem was also encountered by Hopper (unpubl. man.). Critical analyses of floral-pollinator morphometrics, the nature of the floral attracting cues, and behavior of the animals at the flowers will be necessary to resolve these problems.

Long-lived coadapted pollinators such as nonflying mammals and birds must have a continuous supply of nectar and pollen. These resources are provided by plants through temporal partitioning of the flowering periods in a given community. A cursory inventory of the Umagallee study site showed that *Banksia attenuata*, whose pollen predominated both the pollen loads and fecal samples of *Tarsipes*, was blooming on the study site. In addition the following species, perhaps pollinated by nonflying mammals (but not then in flower), also occurred on the study site: *Banksia dryandroides*, *B. prostrata*, *B. quercifolia*, and *B. sphaerocarpa*; *Dryandra sessilis* and *D.* cf. *plumosa*. Insufficient phenological data are available to determine if the flowering periods of these species overlap properly, or if the plants are present in sufficient densities to provide the continuous supply of nectar and pollen necessary to attract and maintain nonflying mammal pollinators. Species in other genera on the study site, however, may also be pollinated by nonflying mammals, e.g., *Beaufortia*, *Callistemon*, *Calothamnus*, *Conospermum*, *Eucalyptus*, *Hakea*, *Isopogon*, *Melaleuca*, *Petrophile*, *Pimela*, and *Regelia*. Monitoring the pollen loads and fecal contents at two to four week intervals for a year should elucidate the changing food resources of nonflying mammal pollinators, and a permanent marking system should indicate if local migration to new floral resources is periodically necessary. Considerable data could be obtained regarding plants putatively pollinated by nonflying mammals by noting the behavior of captive animals when presented with the flowers of various species (Vose, 1972).

Because the flora of the coastal region of southwestern Australia (the southwest province) has an apparently high percentage of bird- and nonflying mammal-pollinated flowers, distinct seasonality of blooming should be reduced so that a constant food source is available. This feature, in fact, was noted for this flora decades ago by Diels (1906). Interestingly, the distribution of *Tarsipes* is virtually restricted to this vegetative zone (Vose, 1972). *Banksia* (ca. 70 species) and *Dryandra* (ca. 80 species) are probably the most important genera involving nonflying mammal pollination, but *Eucalyptus* (ca. 450 species) needs further study in this regard. We estimate that at least half the banksias and most dryandras (probably the largest endemic west Australian genus) are pollinated by nonflying mammals. Furthermore, dryandras flower mostly during winter when fewer plants are blooming. A monthly calendar of bee plants for the coastal plain (Smith, 1969)

shows that at least one species of *Banksia*, *Dryandra*, or *Eucalyptus* is in flower each month of the year.

The extent of pollination by nonflying mammals in the rich flora of southwestern Australia is unknown. Rourke & Wiens (1977) listed 11 marsupials and 1 placental mammal which were reported to take nectar from flowers. The only data on actual pollen loads on Australian mammals are in a paper by Carpenter (1978) on *Rattus fuscipes*, the material reported here, and additional data for *Tarsipes* obtained by Hopper (unpubl. man.). Additional information of anecdotal origin is available, however, which we mention with the hope that it will stimulate further studies.

R. Young (pers. comm.) has observed *Pseudocheirus peregrinus* taking nectar from *Eucalyptus* flowers. M. Morcombe (pers. comm.) has observed *Mus mustelloides* on the spikes of *Banksia attenuata*, and also reports that *Petaurus breviceps* takes nectar from flowers in captivity. D. Kitchener (pers. comm.) suggests that the following animals might also play a role in pollination: *Melanomys* sp.; *Ningaui timealeyi, N. ridei*; *Pseudomys albocinereus, P. occidentalis*; and *Smithopsis* sp. T. Milewski (pers. comm.) also suggests *Pseudomys* as a potential pollinator and points out that the approximately six species are habitat specific in sclerophyll shrub communities, but the factors restricting their distribution are unknown.

To our knowledge *Tarsipes* is the only nonflying mammal known to have coevolved structural and, presumably, physiological and behavioral characteristics which adapt it to a diet of nectar and pollen. Preliminary observations of liquid preserved pygmy possums (*Cercartetus concinnus*) in the Western Australia Museum suggest it also has a brushed tongue, but detailed studies are needed for confirmation. Wakefield (1963) states that the diet of pygmy possums is restricted to nectar, insects, and other arthropods; a photograph shows it foraging on the flowers of *Eucalyptus leucoxylon*.

Utilizing skins in the Western Australia Museum, the heads of some of the animals mentioned above were tested for pollen loads. Since skins are normally cleaned prior to accessioning, the chances of finding pollen would not seem high. Nevertheless, pollen tentatively identifiable as *Banksia attenuata* was found on *Smithopsis*, and pollen was also recovered from *Cercartetus*. The technique could be valuable to determine potential nonflying mammal pollinators and the plants they might visit.

The number and groups of plants adapted for pollination by nonflying mammals in southwestern Australia is largely unknown. In addition to those mentioned previously and those summarized by Rourke & Wiens (1977) from various sources, the following suggestions are offered by A. George (pers. comm.): *Baxteria* (Xanthorrhoeaceae), *Conostylis* (Haemodoraceae), those species with semicryptic ground flowers; *Darwinia* (Myrtaceae), a few ground-flowering species, e.g., *D. speciosa*; *Lamarchea* (Myrtaceae), a monotypic ground-flowering species; *Verticordia* (Myrtaceae), perhaps *V. cauliflorous* and *V. penicellatus*. In addition the genus *Brachysema* (Papilionaceae) has several geoflorous species that might be pollinated by nonflying mammals. *Brachysema* and a number of other genera, however, have ground-flowering species which appear to be bird

pollinated. We recognize that geoflory, per se, is not necessarily an indication of pollination by nonflying mammals.

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ROGGEVELDIA, A NEW GENUS OF SOUTHERN AFRICAN IRIDACEAE-IRIDEAE[1]

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ABSTRACT

Roggeveldia is a new genus recently discovered in the western Karoo, Cape Province, South Africa. Its vegetative morphology, including a cormous rootstock and single leaf is like that of *Moraea* and *Homeria* (Iridoideae-Irideae). Floral characters, anomalous for this alliance, include entirely free stamens and simple terete style branches, features characteristic of Sisyrinchieae, especially the South African *Bobartia*. Floral similarity is probably a result of convergence. Chromosome number in *R. fistulosa* is $n = 6$, which is consistent with numbers in *Moraea* and *Homeria*, but not with Sisyrinchieae.

Roggeveldia is a new genus of African Iridaceae, subfamily Iridoideae. It is probably closely related to *Moraea* and *Homeria* (Irideae-Homeriinae), having a cormous rootstock of a type characteristic of these genera. While *Roggeveldia* conforms to *Moraea* and *Homeria* in its corm, leaf, and general facies, it is remarkable in having long, undivided style branches alternate with the anthers, and free stamens, the filaments not even coherent at their base. Its flower, which also has subequal, outspread tepals, is unique among African Irideae. Of the African genera of Iridaceae-Iridoideae, the flower of *Roggeveldia* is most like *Bobartia*, a rhizomatous genus usually assigned to the predominantly New World Sisyrinchieae, a tribe quite distinct from the Old World Irideae, and one sometimes accorded subfamilial status. Before discussing the relationships and possible origin of *Roggeveldia*, the morphology is described in some detail and the requisite formal taxonomic information presented.

MORPHOLOGY

ROOTSTOCK

The corm is of the single internode type (Lewis, 1954; DeVos, 1977) found in all genera of Homeriinae (Goldblatt, 1976b). The corm, a swollen lateral bud, comprises a single internode with an apical bud primordium and the roots emerge from the bud base on sprouting. The tunics are composed of tough, dark brown reticulate fibers, resembling the type found in several species of *Homeria* and *Moraea*.

LEAVES

A single membranous cataphyll sheaths the base of the leaf, and extends shortly above the ground. In older plants the cataphyll becomes dry and pale brown, but remains intact. The produced leaf is solitary, terete, and hollow. At its apex there is a short, peculiar conical structure found invariably at the leaf

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apices of *Moraea* and *Homeria,* whether terete or bifacial. The leaf is very long at flowering time and usually dry, and broken in the upper half.

STEM

The stem is erect, composed of several internodes, and bears a few branches from the upper nodes. All nodes, with or without branches, bear short sheathing bractlike leaves which are dry and pale, with dark attenuate apices.

INFLORESCENCE

Each inflorescence contains several flowers, which bloom sequentially, a few days apart. The flowers are enclosed by large opposing bracts or spathes, typical of Iridoideae, including Sisyrinchieae, but the outer spathe margins are united in the lower part, a feature known only in genera of Homeriinae.

FLOWERS

The flowers are small, with free, subequal spreading tepals. All six tepals are shortly unguiculate, with the ascending claws forming a shallow central cup. The stamens are straight, slightly inclined and entirely free, with slender filaments. After anthesis the anthers tend to curve inwards from the apex (Fig. 1B). The style is short and filiform and bears three long slender branches which extend outwards between the filaments. Fruits are not known.

CHROMOSOME NUMBER

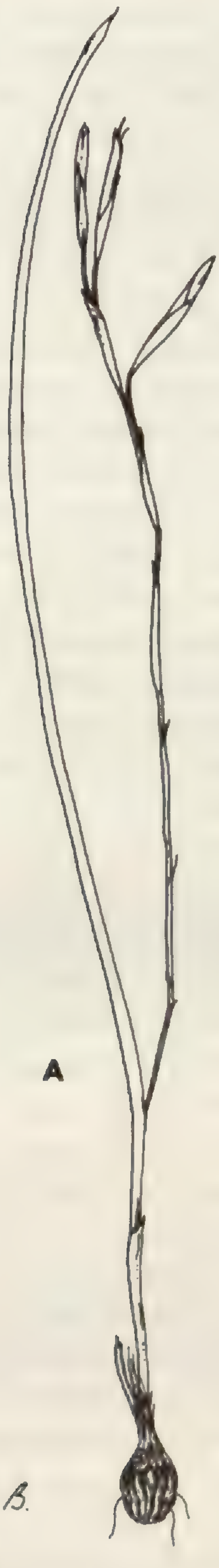
The diploid number is $2n = 12$. The chromosomes are quite large, ranging from 5 to 7μm (Fig. 1C). The largest pair is almost metacentric, and the remaining chromosomes are acrocentric. The next to smallest pair have large satellites, while a pair of longer acrocentrics have an inconspicuous secondary constriction near the end of the longer arm.

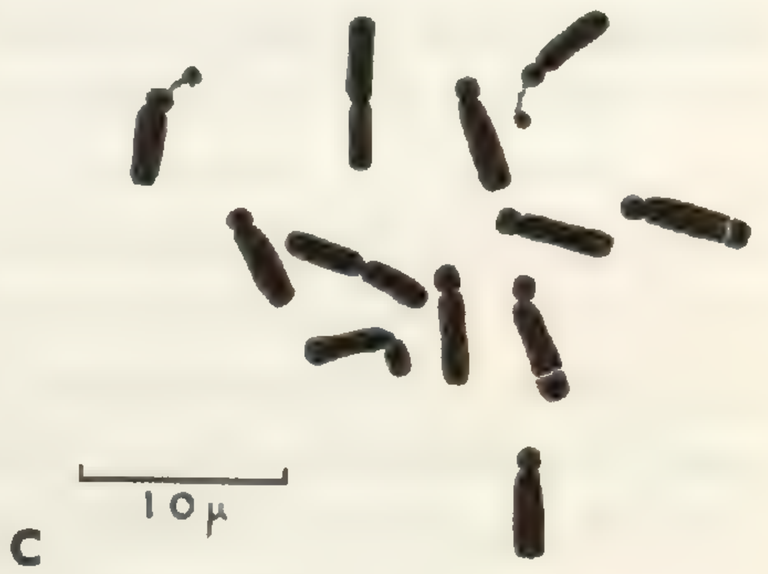
TAXONOMY

Roggeveldia fistulosa Goldblatt, gen. et sp. nov. TYPE: South Africa, Cape, hills near Blomfontein farm between Calvinia and Middelpos, *Goldblatt 4163* (MO, holotype; K, NBG, isotypes).—FIG. 1.

Planta solitaria, 30–50 cm alta. Cormus 1–1.5 cm in diametro, tunicis fibris atrobrunneis. Folium unum, teres, fistulosum, caulis excedentis. Caulis erectus, nodis bracteas attenuatas ferentibus, ramosus. Spatha 3–3.5 cm longa. Flores stellati, fugacei, caerulei, luteo-aurantiacis notatis; tepala subaequalia 1.6–1.8 mm longa, unguis 2 mm longis. Filamenta libera, 4 mm longa; antherae ca 4.5 mm longae, erectae, sed post anthesis incurvatae. Rami styli filiformes, indivisi, antheris alternati, inter filamenta extensi.

Plants solitary, 30–50 cm high. Corm 1–1.5 cm in diameter with tunics of dark brown, wiry fibers. Cataphyll dry to membranous, entire. Leaf solitary, terete, hollow, usually straight, to 3 mm in diameter and longer than the stem. Stem 30–50 cm high, erect, bearing bracts at the nodes, and branching in the upper part; bracts 2.5–3.5 cm long, dry, pale below and with a dark attenuate apex. Spathes





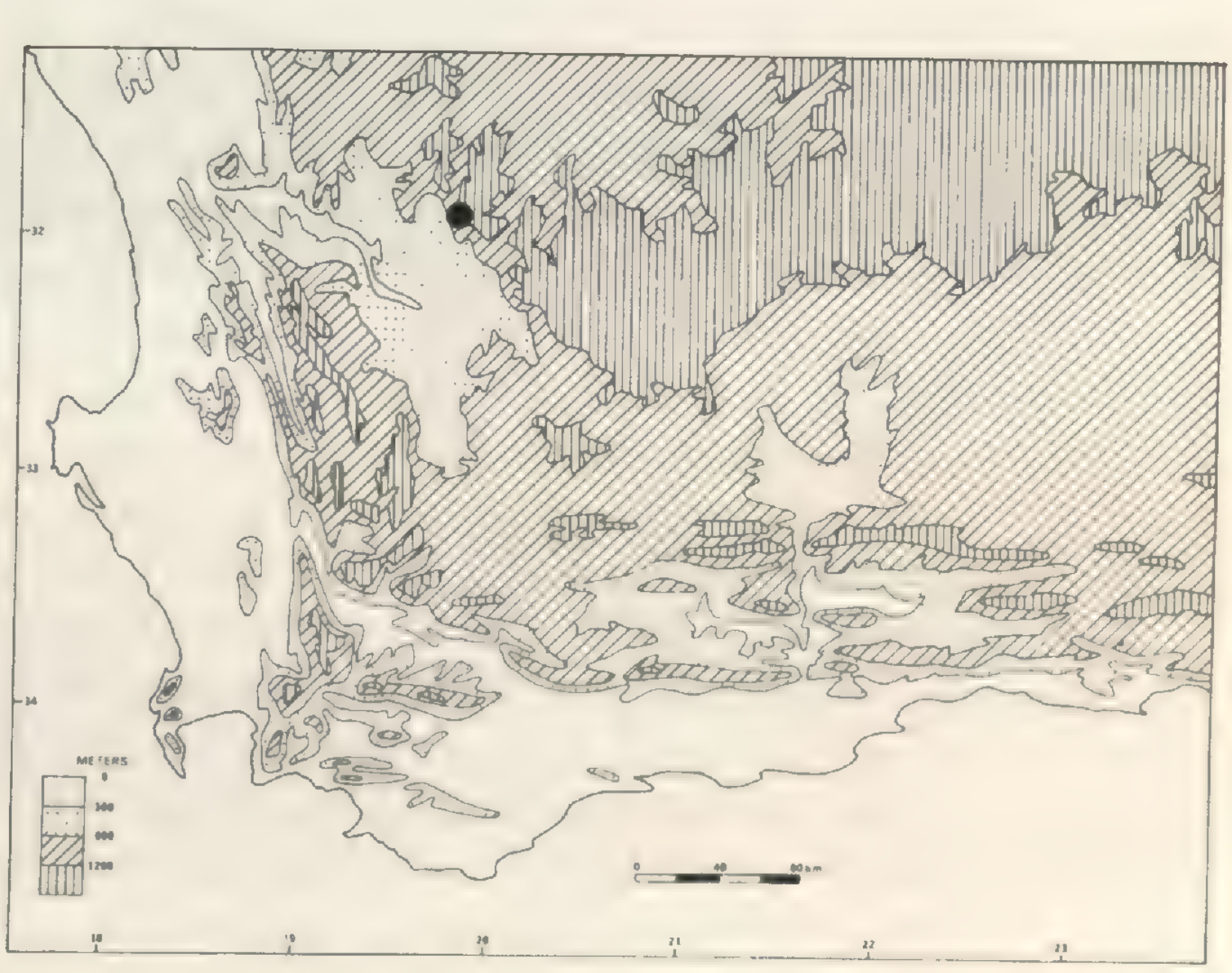


FIGURE 1. Morphology and distribution of *Roggeveldia fistulosa*.—*A*. Habit, ×½.—B. Flower, life size.—C. Mitotic metaphase.

3–3.5 cm long, the outer ca. ⅔ as long as the inner, herbaceous or drying from above, the apex dark brown and attenuate. Flowers stellate, fugaceous, lasting from 4:00–7:00 P.M.; blue with yellow orange nectar guides at the base of the tepal limb; tepals subequal, 1.6–1.8 cm long, the inner whorl slightly smaller, unguiculate, the claw 2 mm long, ascending, the limb outspread. Filaments ca. 4 mm long, free to the base; anthers ca. 4.5 mm, straight in bud, becoming

incurved after anthesis. Ovary ca. 3 mm long; style filiform, 2.5–3 mm long, the branches only 3, slender, ca. 2.5 mm long, outspread, extending between the filaments. Fruit unknown. Chromosome number $2n = 12$.

Flowering time: December.

Distribution: known only from the edge of the Roggeveld escarpment between Calvinia and Middelpos in rocky places with mountain renosterbos vegetation (Fig. 1).

This species was, to my knowledge, first collected in 1976, when I found it while collecting in the Roggeveld between Calvinia and Middelpos. It was first noted during October, when I found only the peculiar leaves. Much later in December, at the beginning of summer, I collected flowering stems, which in the late afternoon at about 4:30 P.M., produced small blue flowers. Although there seemed to be many plants in the immediate area, I could locate only a few in bloom, hence the scanty type gathering. I have found no trace of *Roggeveldia* other than in the immediate area of the original collection, a place around which other interesting endemic Iridaceae have been discovered (Goldblatt, 1979), notably *Babiana virginea* Goldbl., *Ixia thomasiae* Goldbl., and outlying populations of *Moraea unguiculata* Ker and *Hexaglottis lewisiana* Goldbl.

DISCUSSION

Roggeveldia has the characteristics of genera from two apparently quite distinct tribes or even subfamilies. It has flowers most resembling *Bobartia*, regarded as a member of tribe Sisyrinchieae, which is sometimes accorded subfamilial rank, but vegetative parts like those of Irideae-Homeriinae. *Roggeveldia* is not in my opinion in any way a link between these tribes, but seems to me almost certainly a genus of Homeriinae which has an apparently primitive type of flower. This may be the retention of an ancestral character, or, more likely, a reduction and simplification of the flower type found in other genera of this assemblage. In the following discussion I will outline my reasons for this conclusion.

If *Roggeveldia* is related to *Bobartia* (and presumably Sisyrinchieae) as suggested by the floral structure, then one is forced to assume the independent evolution of a very complex type of corm similar not only in general, but matching in every detail the corms in genera such as *Moraea* and *Homeria* of Homeriinae. The leaf of *Roggeveldia* is somewhat specialized in being terete and hollow, an unusual feature, but it is deciduous and also has the peculiar apical appendage as found in other Homeriinae, whereas all *Bobartia* species are evergreen, and their leaves, whether terete or flat, have no modified apex. The jointed and branched stem, with sheathing attenuate bracts are typical of Homeriinae and unlike *Bobartia*, in which the only two branched species, *B. lilacina* Lewis and *B. gladiata* Lewis, both have green obtuse bracts subtending branches. Unbranched species of *Bobartia* have stems of a single internode and thus lack stem bracts.

Cytologically, *Roggeveldia*, $n = 6$, accords well with Homeriinae, where, although a base number of $x = 10$ is believed to be ancestral (Goldblatt, 1976a), $n = 6$ predominates in *Moraea* and is basic in *Homeria* and *Hexaglottis*. *Bobartia* in contrast has $n = 10$ (Goldblatt, 1971; Strid, 1974). The karyotype of *Roggeveldia* matches best those of *Moraea* section *Polyanthes*, species of which

have $n = 6$ and a karyotype of either 6 acrocentric pairs or 5 acrocentrics and one submetacentric. *Homeria* species with $x = 6$ have all the chromosomes strongly acrocentric.

Assuming that my contention that *Roggeveldia* is a true member of Homeriinae is correct, one of the following logically follows. Either the *Bobartia*-type flower evolved independently in *Roggeveldia* or it is a primitive feature of ancestral, now extinct Homeriinae, retained in this genus alone. In order to explore this it is necessary to analyze the patterns of variation in *Moraea*, *Homeria*, and their allies. I have suggested (Goldblatt, 1976b) that *Moraea*, the least specialized genus of Homeriinae was derived from a *Dietes*-like ancestor (Irideae-Iridinae). *Dietes* is evergreen, and has equitant large leaves, a thick persistent rhizome and a flower with spreading tepals, usually free stamens and large petaloid style branches with forked crests. The base number is $x = 10$.

In *Moraea*, a large genus of some 100 species, and other genera of the subtribe, the rootstock is a corm, the plants are deciduous, and the leaf is typically bifacial and channeled, but occasionally terete. *Moraea* is distinguished in the subtribe by its flattened petaloid style branches with transverse styles and dimorphic tepal whorls. Highly ramified and multileafed species of *Moraea* have unspecialized flowers, are presumably primitive, and have a base number of $x = 10$ (or 9) (Goldblatt, 1976a). Specialized species have only a single leaf, reduced branching, and mostly $x = 6$. Among this group are some species with narrow style branches and very short or vestigial crests, and subequal tepals, features which accord with characteristics of the related genera *Homeria* and *Rheome* (Goldblatt, in prep.). Other species of *Homeria* have slender style branches which appear to be derived from *Moraea* directly, by reduction and simplification of certain floral features, and it is likely that this trend occurred in several lines in *Moraea*, giving rise to several species of *Moraea* section *Polyanthes*, notably *M. crispa*, *M. alba* and *M. polyanthos* (Goldblatt, in prep.), as well as *Homeria* and *Rheome*.

One other genus is relevant to this discussion, *Hexaglottis*, a small genus much resembling *Homeria*. In *Hexaglottis* the stamens are only partially united, while style branches are each deeply divided into two long branches which extend horizontally between the filaments.

The point of this exposition of the morphology in the *Moraea-Homeria* alliance is that the general evolutionary pattern here appears to be of reduction of several independent features: leaf number, branching, tepal whorl dimorphism, and style branch size and complexity. The style branches vary from broad, petaloid, and crested to narrow and linear with reduced crests and ultimately to a filamentous state either with forked apices (*Homeria* or *Rheome*) or forked to the base (*Hexaglottis*). The style branch reduction usually is accompanied by decreasing differences between inner and outer tepal whorls.

Roggeveldia can, in the reduction pattern described above, be easily interpreted as a plant in which one further step in this progression has occurred. It resembles most closely *Moraea crispa*, and compared to this species, the processes required to produce the *Roggeveldia* flower may be outlined as follows. First, the filaments, which range in *M. crispa* from free near the apex only, to free for two-thirds their length, become entirely separate. Second, the narrow

but flattened style branches of *M. crispa* which lie along the anthers and are bilobed apically would lose their flattness and slight terminal lobing, becoming terete and filiform. Third, the style arms, no longer flat, would lose their position lying against the anthers, and by twisting through some 30–60 degrees, come to lie in the space between each anther. *Moraea crispa* is so similar in other respects that it can barely be distinguished from *Roggeveldia*.

There seems little doubt that *Roggeveldia fistulosa* merits generic recognition as it has characteristics of several different genera in unique combination. It cannot be assigned to an existing genus without major, and to my mind, unnecessary redefinition of the African members of Iridoideae. Despite its very simple and apparently primitive flower, the interpretation of available evidence makes it reasonable to assume that it was derived from species like *Moraea crispa* of *Moraea* subgenus *Vieusseuxia* by an evolutionary process of reduction of complex floral parts. Vegetative morphology and cytology entirely accord with this hypothetical phylogeny. Floral similarities between *Roggeveldia* and *Bobartia*, however striking, are believed to be due to convergence.

POSTSCRIPT ON BOBARTIA

Bobartia, a small genus of some 15 species (Strid, 1974) is generally regarded as a member of tribe Sisyrinchieae (or Sisyrinchioideae). The tribe comprises mainly New World and Australasian genera, *Bobartia* being the only African member. Placement of *Bobartia* here seems anomalous on phytogeographic grounds and, with the exception of its unspecialized flower, *Bobartia* does not conform well with other genera of Sisyrinchieae. The discovery of just this type of flower in *Roggeveldia*, almost certainly a very specialized genus of Irideae, makes it reasonable to question the apparent primitiveness of the *Bobartia* flower and hence the systematic position of this genus. It seems at least possible that *Bobartia* may have been derived from African relatives of Irideae with more complex flowers in the same way that the *Roggeveldia* flower is presumed to have evolved. The genus *Dietes*, which has a similar thick woody rhizome, evergreen leaves, and a basic chromosome number of $n = 10$, the same number as in *Bobartia*, should be considered in particular, as possibly close to the ancestral type for *Bobartia*.

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SAVANNOSIPHON GEN. NOV., A SEGREGATE OF *LAPEIROUSIA* (IRIDACEAE-IXIOIDEAE)[1]

PETER GOLDBLATT[2] AND W. MARAIS[3]

ABSTRACT

The central African species previously known as *Lapeirousia euryphylla* Harms is transferred to a new genus *Savannosiphon*. Comparisons of *Savannosiphon* with *Lapeirousia*, *Anomatheca* and other Ixioid Iridaceae lead to the conclusion that *Savannosiphon* is allied to *Lapeirousia* and to *Thereianthus* and *Micranthus*, and it should be placed with these genera in tribe Watsonieae. A chromosome number of $n = 7$ has been found in *S. euryphyllus*.

It has been the impression of the authors for several years since we separately began systematic studies of *Lapeirousia* and *Anomatheca* (Goldblatt, 1972; Marais, unpubl.) that the fairly well-known tropical African *Lapeirousia euryphylla* Harms did not belong in *Lapeirousia*, nor did it seem to conform well with the related *Anomatheca*. This opinion was evidently shared by Diels (1930) who placed *L. euryphylla* in *Acidanthera*, a genus nomenclaturally synonymous with *Gladiolus*, though other species at times assigned to *Acidanthera* are now considered to belong to several other genera of Iridaceae-Ixioideae (Lewis, 1941). More recently, we have had the opportunity of growing this plant and close observation has strengthened the conviction that *L. euryphylla* is misplaced. Chromosome counts, made from cultivated material, have also lent some support for our view that *L. euryphylla* should be removed from *Lapeirousia*. We have consequently decided to describe the new genus *Savannosiphon* to accomodate *L. euryphylla*.

CHARACTERISTICS OF *SAVANNOSIPHON EURYPHYLLUS*

Savannosiphon euryphyllus is entirely tropical in distribution (Fig. 1), extending from Shaba Province (Geerinck et al., 1972) of Zaïre and Tanzania, southward through Zambia, Malawi, and northern Mozambique. It has round-based corms (Fig. 1C) which are depressed globose in shape, with often quite coarsely fibrous tunics. Interestingly, the corms of *Savannosiphon* originate from axillary buds, as described by DeVos (1977) in *Lapeirousia*, *Watsonia*, *Thereianthus*, and *Micranthus*, in which feature these genera constitute an apparently unique group in subfamily Ixioideae. *Savannosiphon* has only a few leaves (Fig. 1A), the lowest one inserted on the stem near the ground and others inserted at nodes above ground level. The leaves are unusual, being soft in texture and corrugate-plicate, a feature occurring sporadically in Ixioideae, but not found in *Lapeirousia* or *Anomatheca*. The stem is more or less terete below but flattened and 2-winged below the inflorescence and erect and unbranched. It bears only a few flowers, a two- to six-flowered spike being usual. The bracts are long and herbaceous, but enclose only part of an extremely long, slender, cylindrical perianth tube. The flowers

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are pure white, apparently scentless, and essentially actinomorphic. They last only about 12 hours, opening at sunset, and fading in the early morning, so that by sunrise they are limp and partly collapsed. The stamens are somewhat unusual in being enclosed in the perianth tube, and only the upper ends of the anthers sometimes protrude from the narrow part of the tube into the wider throat. The style branches are deeply divided.

The chromosome number is $n = 7$ and the karyotype comprises three long and five medium-short to short, acrocentric chromosomes (Fig. 1D). The chromosome number and karyotype are clearly quite unlike the *Anomatheca* pattern (Goldblatt, 1972) where $x = 11$. Nor does the karyotype of *Savannosiphon* bear much resemblance to any recorded pattern in *Lapeirousia* (Goldblatt, 1972, 1980), which is however rather variable in karyotype as detailed in the following section.

SURVEY OF *LAPEIROUSIA* AND *ANOMATHECA*

Lapeirousia, a genus of some 25 species, ranges almost throughout sub-Saharan Africa, occurring from Nigeria and Ethiopia to the Cape Province of South Africa. Its most characteristic feature is a flat-based, conical to bell-shaped corm, the tunics of which are initially entire, and often tough and woody, though the outermost layers may become irregularly broken or fibrous. Most often species have a single produced leaf, which is often characteristically ribbed, though several, flat leaves are present in a few species. Stems are often flattened, and angular, and usually branched. The inflorescence is either a diffuse panicle or a spike, or by reduction a basal rosette. Floral bracts are herbaceous and fairly short in the species with panicles, or quite long in some spicate or rosette species. Flowers range from stellate and actinomorphic to strongly zygomorphic, either with short or extremely long perianth tubes. Style branches are typically deeply divided but undivided style branches are recorded in two species.

Anomatheca is a smaller genus, comprising only five species, which extends from south-tropical Africa to the Cape. The corms are round based, and conic to globose, with soft-textured fibrous tunics. Leaves are flat, soft in texture, numbering from two to several in distichous arrangement, and the stems are usually terete, but are angled in one species. The bracts are short and herbaceous, and the inflorescence is typically an inflexed secund spike, although in *A. fistulosa* each branch of the inflorescence bears a single flower. Flowers are zygomorphic with slender or tapering perianth tubes. As in *Lapeirousia*, the style branches are deeply divided. *Anomatheca* is, we believe, very closely related to *Freesia*, and shares with it all characters except that in *Freesia* the perianth tube has a slender cylindrical basal part and a wide cylindrical upper part. Species of *Freesia* always have a prominently flexed inflorescence, so that the spike is more or less horizontal to the ground. The corm differences between *Anomatheca* and *Freesia*, on the one hand, and *Lapeirousia*, on the other, are considered fundamental and suggest that *Lapeirousia* may not even be particularly closely related to *Anomatheca* and *Freesia*.

Cytological differences reinforce the morphological distinctness of *Lapeirousia* and *Anomatheca* (Goldblatt, 1972). Both *Anomatheca* (and the related *Freesia*) have a basic chromosome number of $x = 11$, the karyotype comprising small, more or less uniform-sized chromosomes. In *Lapeirousia* the cytological situation

FIGURE 1. Morphology, distribution, and chromosomes of *Savannosiphon euryphyllus*.—A. Aerial parts (×1/2).—B. Section of flower (life size).—C. Corm in side and basal view (×1/2).—D. Mitotic metaphase.

is less clear. Species from the winter rainfall region of South Africa have a pronounced bimodal karyotype with a pair of very large chromosomes and numerous very small pairs with haploid numbers in the range $n = 10$, 9, and 8. In tropical African species (Goldblatt, 1980) the bimodal karyotype has been found in *L. caudata* and *L. odoratissima*, both $n = 8$. Other species have a normal karyotype with *L. schimperi*, $n = 5$, and members of the *L. erythrantha* complex variable, having $n = 4$ in *L. coerulea* and *L. rhodesiana*, $n = 6$ in *L. bainesii*, and a bimodal karyotype with $n = 10$ in *L. vaupeliana*, a species possibly conspecific with *L. bainesii*.

RELATIONSHIPS OF *SAVANNOSIPHON*

In the more fundamental taxonomic characters of Ixioideae, such as corm and tunic, *Savannosiphon* appears discordant with *Lapeirousia*, the latter having a corm unique in the Iridaceae in its symmetrical bell shape with a flat base, and tough woody to fibrous tunics. In leaf form *Savannosiphon* is also rather different from *Lapeirousia*, none of its species having the broad, corrugate-pleated leaf of *Savannosiphon*. *Lapeirousia* and *Savannosiphon* are similar in that each usually has a single produced leaf, inserted near the base of the stem, and not on the corm. The inflorescence and flower of *Savannosiphon* suggest few generic relationships, except that the style branches are deeply divided, a characteristic of only a few Ixioid genera. The night-blooming fugaceous flowers are reminiscent of *Hesperantha*, but nothing else suggests a relationship. The enclosed stamens in *Savannosiphon*, very unusual in Iridaceae, are known only in a few isolated species of *Ixia* and *Hesperantha*.

The stigma character, considered of major taxonomic importance in Ixioideae, forces us to consider *Savannosiphon* related to genera with this feature, there being no good reason to disregard the significance of the divided style branches in this case. The main groups of Ixioideae with divided style branches, as treated by Goldblatt (1971) are *Anomatheca* and *Freesia* (Freesiinae), *Lapeirousia* (Lapeirousiinae), *Watsonia*, *Thereianthus* and *Micranthus* (Watsoniinae), and *Romulea*, *Syringodea* (and the Northern Hemisphere *Crocus*) (Crocinae). For a variety of reasons, including greatly modified leaves, and reduced habit, the Crocinae need not be considered here.

Of the three remaining groups *Lapeirousia* has already been dealt with, since it is the genus from which we are removing *Savannosiphon euryphyllus*. It is also the only genus here which has flat-based corms. Freesiinae have rather soft-textured fibrous corm tunics, and distichously arranged leaves inserted on the corm. The corms are of the several internode type and are derived from an apical bud. Corm and leaf form and development are thus rather different from that of *Savannosiphon*.

The remaining group, Watsoniinae, has round-based corms, which originate from axillary buds in seasons when blooming occurs (DeVos, 1977). In *Micranthus* and *Thereianthus*, both Cape genera of this subtribe, corms are typically of a single internode, and the basal leaf is single, inserted on the stem near ground level. *Savannosiphon* thus has a leaf and pattern of corm development very similar to *Micranthus* and *Thereianthus*. Other features of the latter two genera such as dense, several- to many-flowered spikes, small flowers, small dry bracts,

and spindle-shaped seeds suggest that they are not directly related to *Savannosiphon*. *Watsonia* also has similar corm development, although corms are usually of more than one internode, but it has several distichously arranged leaves, of characteristic tough texture. The remaining genus of this subtribe, *Pillansia*, is very different in having a paniculate inflorescence and simple style branches.

In summary, it seems that *Savannosiphon* does not accord with any of the existing groups of genera having divided style branches, but it does have similar leaf insertion and corm development of *Lapeirousia* and *Micranthus*. It is likely that *Savannosiphon* does belong in this general area of the Ixioideae, perhaps between Lapeirousiinae and Watsoniinae, if these retain their narrow circumscriptions. With subfamily as the major subdivision of Iridaceae, the best way to reflect the relationships of these genera would be to recognize a tribe Watsonieae to accommodate those genera with divided style branches and axillary corm development, i.e., subtribes Lapeirousiinae and Watsoniinae. Consistent treatment suggests the recognition also of a subtribe for *Savannosiphon*, though there seems little need at the present for such detailed classification.

SYSTEMATICS

Savannosiphon Goldblatt & Marais, gen. nov. TYPE SPECIES: *S. euryphyllus* (Harms) Goldblatt & Marais.

Planta 15–30 cm alta, *cormi* ca. 1 cm in diametro, ad basin versus rotundati. *Folia* producta (1–)2–3, ensiformia, corrugata. *Caulis* bialata supra simplex. *Inflorescentia* spicata 1–4(–6) floribus praedita; *bracteae* herbaceae 2, exterior grandior, 4–15(–30) cm longa. *Flos* albus, tubo perianthio longissimo, tepalis expansis. *Stamina* symmetrica. *Stylus* filiformis ramis perfurcatis.

Plants moderate in size, 15–30 cm tall; stoloniferous. *Corms* subglobose, round based, axillary; single internode, ca. 1 cm in diameter; tunics of medium to coarse fibers, initially forming an entire layer. *Produced leaves* 1–2(–3), the lowermost basal and inserted near ground level, the upper usually cauline and smaller, ensiform, corrugate-plicate, 10–40 cm long, 15–45 cm wide. *Stem* erect, simple, terete towards the base, flattened and 2-winged below the inflorescence. *Inflorescence* a 1–4(–6)-flowered spike; outer bract herbaceous, 4–15(–30) cm long, the inner 3–5.5 cm long, but usually ± subequal. *Flowers* white, actinomorphic, odorless, night blooming; perianth tube 8–12.5 cm long, cylindrical and expanded only at the apex; tepals 4–5 cm long, acute, the upper sometimes larger and slightly hooded, the lower spreading to horizontal. *Stamens* symmetrical; filaments inserted on the perianth tube ca. 15 mm below the throat; anthers ca. 10 mm long, apiculate, symmetrically disposed, facing outwards, entirely included or the upper part emerging from the narrow part of the tube. *Ovary* ca. 6 mm long, oblong; style slender, dividing near the apex of the anthers, the branches deeply forked. *Capsule* ca. 15 cm long, ovoid; seeds round, shiny, ca. 2 mm in diameter. Chromosome number $2n = 14$. (Fig. 1D).

Flowering time: Summer, mid-rainy season, January–February.

Distribution: Southeast and central Africa, including Shaba Province, Zaïre, Zambia, southern Tanzania, Malawi, and northern Mozambique.

The only species is *Savannosiphon euryphyllus* (Harms) Goldblatt & Marais,

comb. nov., based on *Lapeirousia euryphylla* Harms, Bot. Jahrb. Syst. 28: 366. 1900. A synonym is *Acidanthera euryphylla* (Harms) Diels, Engler & Prantl, Nat. Pflanzenf. ed. 2, 15a: 492. 1930.

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PRELIMINARY CYTOLOGY OF AUSTRALASIAN IRIDACEAE[1]

PETER GOLDBLATT[2]

ABSTRACT

Native Australasian Iridaceae are poorly known cytologically with only *Libertia*, $x = 19$, well studied. In other genera *Patersonia* is shown to have $n = 11$ (not 12 as previously reported), 21 and 31, *Diplarrhena* has $n = 15$–16, and *Orthrosanthus laxus*, a high polyploid, $n = 75$–80. The only non-African species of *Dietes*, *D. robinsoniana*, from Lord Howe Island, has $n = 10$ which agrees with $x = 10$ known for the African species. An artificial hybrid *D. robinsoniana* × *D. iridioides* also has $n = 10$. Affinities of the Autralasian Iridaceae are discussed in relation to the cytology and morphology.

There are five or perhaps six native genera and some 26 species of Iridaceae in Australasia, few compared to the other southern continents where the family is well represented. Two Australasian genera, *Libertia* and *Orthrosanthus* are shared with South America and one, *Dietes*, with Africa, while *Diplarrhena*, *Patersonia*, and also *Isophysis* (if this is admitted to the family) are endemic. *Patersonia* actually extends to New Guinea and Borneo, though it is centered in temperate Australia.

The affinities of the endemic genera are not clear, while the relationship of the Australasian species of *Dietes* to the rest of this essentially African genus has been the subject of considerable interest. Cytology has been of great value in interpreting relationships of Iridaceae in Africa (Goldblatt, 1971, 1976a) and seems likely to be of value in the New World also. The Australasian species and genera are hardly known cytologically except for *Libertia* (Hair et al., 1967), and with this in mind I have undertaken this study. Results to date have been somewhat meager but seem worth reporting, in spite of remaining gaps in the record. Hopefully results will stimulate further investigation of the family in Australasia.

MATERIALS AND METHODS

Seeds and plants of native Australian species were obtained from Kings Park and Botanic Garden, Perth; from Winifred Curtis and Desmond Morris, Tasmania; and from the Royal Botanic Gardens, Sydney. The hybrid *Dietes robinsonia* × *D. iridioides* was made by M. Boussard, Verdun, France, from parent plants of wild origin. Unfortunately, with few exceptions material is not represented by vouchers collected in the wild, and I have been able to make vouchers of only the few which grew to flowering at the Missouri Botanical Garden.

All counts were made from mitotic preparations. Root tips obtained from actively growing plants were pretreated in 0.003 M hydroxy-quinoline, fixed in Carnoy's solution, hydrolyzed in 10% HCl for 6 minutes at 60°C and squashed

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TABLE 1. Chromosome numbers in Australasian Iridaceae. Counts in **bold** type are new reports.

Species	Diploid no. 2*n*	Collection Data
Dietes		
D. robinsoniana (F. Muell.) Klatt	**20**	Lord Howe Is., ex Hort. Kew, no voucher.
D. robinsoniana × *D. iridioides*	**20**	(Parents of wild origin) voucher cult. at Missouri Botanical Garden, *Goldblatt 4673* (MO).
Diplarrhena		
D. moraea Labill.[a]	**30–32**	Tasmania, Linda, *Curtis s.n. sub Goldblatt 4674* (MO); Tasmania, Rekuna, *Morris s.n.* (no voucher).
Libertia		
L. puchella (R. Br.) Spreng.	38	New Guinea (Borgmann, 1964); New Zealand (Hair et al., 1967).
L. ixioides (Forst. f.) Spreng.	12*x*	New Zealand (Hair et al., 1967).
L. grandiflora (R. Br.) Sweet	6*x*, 12*x*	New Zealand (Hair et al., 1967).
L. peregrinans Ckn. & Allan	6*x*	New Zealand (Hair et al., 1967).
Orthrosanthus		
O. laxus (Endl.) Benth.	**150–160**	W. Australia, Helena Valley, Perth, *Demarz 7171* (PERTH).
Patersonia		
P. occidentalis R. Br.	24	W. Australia (Goldblatt, 1971).
	22	W. Australia, Perth distr., *Demarz s.n.* (no voucher).
P. sericea R. Br. ex Ker	**22**	New South Wales, Clarence, no voucher or NSW.
P. umbrosa Endl.	**22**	W. Australia, Lort River, *Demarz 4938* (PERTH).
P. fragilis (Labill.) Asch. & Graeb.	**42**	New South Wales, Clarence, *Hind 788* (NSW).
P. sp.	**62**	Tasmania, Murchison highway, *Curtis s.n.* (no voucher).

[a] W. Curtis (pers. comm.) suggests *D. latifolia* Benth. is distinct from *D. moraea* Ladill. in which case the plants above are *D. latifolia*.

in lacto-propionic orcein. Species studied, numbers obtained and collection information is listed in Table 1.

OBSERVATIONS

Dietes

The Australasian species of *Dietes*, *D. robinsoniana*, has a diploid number of $2n = 20$. A hybrid, *D. robinsoniana* × *D. iridioides*, raised by M. Boussard also has $2n = 20$. The African species of *Dietes* are either diploid, $2n = 20$, or tetraploid, $2n = 40$ (Goldblatt, 1971, and unpublished data; Chimphamba, 1974). The karyotypes of the Australasian and African species are similar, with chromosomes of the same size and general morphology. There seems little doubt that *D. robinsoniana* is correctly placed in *Dietes*.

Patersonia

The only previous count in *Patersonia*, $2n = 24$ for *P. occidentalis*, (Goldblatt, 1971) is incorrect. Repeated counts for this species have consistently yielded $2n = 22$. The karyotype comprises fairly small chromosomes ranging from 1.5–3 μm. There are three pairs of larger chromosomes and a pair of conspicuously large satellites. *Patersonia sericea* and *P. umbrosa* also have $2n = 22$, and an identical karyotype, while *P. fragilis* is polyploid with $2n = 42$. Though $2n = 44$ would be expected, I have not been able to demonstrate more than 42 chromosomes. An as yet undetermined Tasmanian *Patersonia* seems hexaploid, but here, although $2n = 66$ would seem likely, I could only count $2n = 62$. Aneuploid reduction may have taken place in these polyploid species if the counts are correct. Clearly, more studies are needed in *Patersonia*, especially in the polyploids. For accurate results in species with higher numbers meiotic studies are recommended.

Diplarrhena

A diploid number of $2n = 30$–32 was obtained for this endemic Australian genus consisting of either one (Geerinck, 1974) or two species (Bentham, 1873; Curtis, pers. comm.). The karyotype consists of fairly small chromosomes, ranging from 1.5–3 μm in size. Doubt as to the correct number is due to difficulty in interpreting two possible small chromosomes of somewhat less that 1μm in length, which may be satellites, though I could not demonstrate any connection between these and any of the larger chromosomes. An exact chromosome count thus awaits further investigation.

Orthrosanthus

One species, *Orthrosanthus laxus*, was examined, which proved to be a high polyploid with the diploid number in the range $2n = 150$–160. Chromosomes are very small and an accurate count will probably be obtained only from meiotic study. The tiny chromosomes are similar in size to those I have seen in the related *Libertia*, which has a base number of $x = 19$ (Hair et al., 1967; Borgmann, 1964).

Discussion

With the exception of *Dietes* and *Isophysis*, the Australasian genera of Iridaceae are believed to be related in a general way to one another and to several New World genera including *Sisyrinchium*, *Tapeinia*, *Chamelum* and their allies. *Isophysis*, with its superior ovary, is rather isolated and is not always accepted as belonging to Iridaceae. It was first associated with this family by Hutchinson (1934). *Dietes*, all but one species of which are African, belongs to Iridoideae-Irideae in Iridinae (Goldblatt, 1976b) (or close to this subtribe), and is allied to the northern temperate genus *Iris*, and to the African *Moraea*. It is intermediate in many ways between these two genera (Goldblatt, 1976a, 1976b).

Libertia, *Orthrosanthus*, and *Diplarrhena* are usually allied with the New World *Sisyrinchium* in Sisyrichieae-Sisyrinchiinae (Diels, 1930). Recently Geer-

inck (1974) placed *Libertia pulchella* in *Sisyrinchium* and suggested that the two genera are very closely related. Chromsosome numbers, however, do not support this treatment, nor do they provide evidence for a particularly close relationship of *Sisyrinchium* with *Libertia* or *Diplarrhena*. *Sisyrinchium* has $x = 9$ ($n = 9, 8, 17$) and its close ally *Phaiophleps* also has $x = 9$, while *Libertia*, with much smaller chromosomes, has $n = 19$, and *Diplarrhena* has $n = 15(-16)$.

Alternative treatments such as that of Pax (1888) place *Diplarrhena* and *Libertia* together in Libertiinae separate from Sisyrinchiinae, with *Orthrosanthus* in Aristeinae, the latter otherwise entirely African. The separation of *Orthrosanthus* and *Libertia* in different subtribes seems unjustified, since both have long style branches, not known in *Aristea* and its close relatives. *Orthrosanthus* seems best placed close to *Libertia*, whether included in Sisyrinchiinae or separated in Libertiinae, a treatment which appears to have merit on the cytological data available to date.

Patersonia, also placed in Sisyrinchieae, is usually referred to Aristeinae (Diels, 1930; Hutchinson, 1934, as Aristeae) which includes the African *Aristea*, the three shrubby South African genera, *Klattia*, *Witsenia* and *Nivenia*, all with $x = 16$, and *Ona*, *Chamelum*, and *Solenomelus* in South America, cytologically unknown. The base number for *Patersonia*, apparently $x = 11$ from this study, suggests no close connection with *Aristea*, though chromosome size is similar. Morphology suggests *Patersonia*'s closest ally may be *Aristea*, both genera having simple styles with expanded stigma lobes. These are fringed in *Patersonia* but entire in *Aristea*. Other features, such as the long perianth tube, united filaments, much reduced inner tepals, and well-developed inflorescence spathes in *Patersonia* argue against anything more than a distant relationship between these genera. Cytological differences appear to reinforce this view. Interestingly, *Patersonia* is the only Australasian or New World genus examined by Cheadle (1964) which has xylem as primitive as that found in *Aristea* and its close African allies *Witsenia*, *Klattia*, *Nivenia*. In this respect *Aristea* and *Patersonia* stand apart from Sisyrinchiinae (*Sisyrinchium*, *Diplarrhena Libertia* and *Orthrosanthus*). Other South American genera placed with *Patersonia* in Aristeinae were not examined by Cheadle, and their relationship to either Sisyrinchinae or Aristeinae must rest on morphology alone.

In summary, it appears from the admittedly meager cytological evidence that *Patersonia*, *Libertia*, *Diplarrhena* and *Dietes* are not especially closely related to one another. *Dietes robinsoniana* clearly belongs in *Dietes* and the relationship of this genus with *Iris* and *Moraea* seems clear; however, for the remainder little more can be said than that they have generally primitive features for Iridaceae and placement in Sisyrinchieae seems reasonable. They do not seem particularly closely related to one another or to genera elsewhere, with the exception of a likely link between *Libertia* and *Orthrosanthus*. Best treatment might be placement in separate subtribes. Association of *Patersonia* with the Aristeinae, especially *Aristea* appears to have some merit but morphology and cytology suggest that this relationship if in fact correct is rather distant, though they may possibly be included within a subtribe.

For the Australian region additional counts would be useful in further elaborating the cytological pattern in *Patersonia*, and a firm count for *Orthrosanthus*

should be particularly valuable in establishing its supposed relationship with *Libertia*. Since *Isophysis* is clearly primitive, if actually in the line leading to Iridaceae, a count would be valuable in further evaluating the position of the genus.

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MISCELLANEOUS CHROMOSOME COUNTS IN ANGIOSPERMS, II. INCLUDING NEW FAMILY AND GENERIC RECORDS[1]

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ABSTRACT

The following chromosome counts are reported: *Ferraria glutinosa* $2n = 40$ (Iridaceae); *Mortoniella pittieri* $2n = 32$ (Apocynaceae); *Nemopanthus mucronata* $2n = 20$ (Aquifoliaceae); *Balanites aegyptica* $2n = 18$ (Balanitaceae); *Balanops australina* $2n = 42$ (Balanopaceae); *Neochamaelea pulverulentum* $2n = 36$ (Cneoraceae); *Wendtia gracilis* $2n = 18$ (Ledocarpaceae); *Grevea eggelingii* $2n = 24$ (Montiniaceae); *Trophis phillipinensis* $2n = 28$ (Moraceae); *Uncarina grandidieri* $2n = 36$ (Pedaliaceae); *Holodiscus discolor* $n = 18$ (Rosaceae); *Meliosma panamensis* $2n = 32$ (Sabiaceae); *Trigonia virens* $2n =$ ca. 20 (Trigoniaceae); *Vochysia lomatophylla* $2n = 22$ (Vochysiaceae); *Teedia lucida* $2n = 38$ (Scrophulariaceae). Counts include three first reports for a family and 10 first reports for genera.

Since the publication of Raven's (1975) review of cytology in relation to angiosperm phylogeny which focused attention on important gaps in the chromosome record, a concerted effort has been made by Raven, myself, and others (Goldblatt, 1976a, 1978; Goldblatt & Endress, 1977) to obtain material of cytologically unknown taxa for study. This paper which presents counts in several rare or taxonomically critical groups, as well as some counts of less importance, conveniently included here, is one of a series arising from Raven's study.

Counts presented here include reports for 15 species, each a different family, and three of which, Vochysiaceae, Trigoniaceae, and Balanopaceae are first records for these families. In addition, first generic reports are presented for *Nemopanthus* (Aquifoliaceae), *Neochamaelea* (Cneoraceae), *Wendtia* (Ledocarpaceae), *Holodiscus* (Rosaceae), *Uncarina* (Pedaliaceae), *Trophis* (Moraceae), *Grevea* (Montiniaceae), *Teedia* (Scrophulariaceae), and *Mortoniella* (Apocynaceae). Significance of the counts obtained in relation to taxonomy or phylogeny is discussed briefly after each count.

Counts recorded as haploid are from pollen mother cells, and those given as diploid are from mitosis in root tips. Methods employed are the same as I have described previously (Goldblatt, 1978).

MONOCOTYLEDONS

IRIDACEAE

Ferraria glutinosa (Baker) Rendle, $2n = 40$. Namibia (South West Africa), Ovamboland, Oshikango, *Rodin 9360* (MO).

Ferraria glutinosa, the only tropical African species of this predominantly

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Southwestern Cape-Namaqualand genus, is evidently tetraploid, this being the first reported count for this species. A base number of $x = 10$ is well established for *Ferraria* in western South Africa, with reports of $2n = 20$ and $2n = 60$ for species from this area (Goldblatt, 1971).

DICOTYLEDONS

APOCYNACEAE

Mortoniella pittieri Woodson, $2n = 32$. Nicaragua, Dept. Chontales, N of Cuapa, *Stevens 6170* (MO).

The count of $2n = 32$ for *Mortoniella* is unusual for Apocynaceae in which $2n = 22$ is frequent, and $x = 11$ probably basic (Raven, 1975). The number in *Mortoniella* probably represents polyploidy on the base of $x = 8$, which has been found in a few genera and is the lowest number recorded for the family.

AQUIFOLIACEAE

Nemopanthus mucronata (L.) Trel, $2n = 40$. U.S.A., Caledonia Co., Vermont, West Burke, *Conant 3408* (MO).

This is the first count for *Nemopanthus*, the monotypic North American member of the bigeneric Aquifoliaceae. The base number for *Nemopanthus*, evidently $x = 20$, is the same as that for *Ilex* (Frierson, 1959; Goldblatt, 1976a) and confirms $x = 20$ as basic for Aquifoliaceae.

BALANITACEAE

Balanites aegyptica (L.) Delile, $2n = 18$. Rhodesia, Chipoli near Shamva, cult. Missouri Botanical Garden, *Goldblatt 4649* (MO).

Previous counts in the monogeneric Balanitaceae are $2n = 18$ and 16 for *Balantes aegyptica* and $2n = 16$ for *B. wilsoniana* (Mangenot & Mangenot, 1957, 1962; Pathak et al., 1949). The count obtained here is undoubtedly $2n = 18$, and suggests that the earlier report of $2n = 16$ in *B. aegyptica* may be erroneous, and possibly also that for *B. wilsoniana*. A base number of $x = 9$ seems likely for Balanitaceae.

BALANOPACEAE

Balanops australina F. Muell., $2n = 42$. Australia, Queensland, State Forest Reserve 607, *Dockrill 1405* (QRS).

This is the first count for *Balanops*, and for Balanopaceae, a monogeneric Australasian family of unknown affinity. The family is commonly placed near the predominantly Northern Hemisphere Fagales, either within this order (Cronquist, 1968) or in a separate order in the Betulales-Fagales line of evolution (Takhtajan, 1969). Dahlgren (1975) tentatively places Balanopales between Fagales and Cunoniales in his Hamamelidanae. The treatment of Thorne (1976) is exceptional in placing Balanopaceae in Pittosporales-Daphniphyllineae, the other family of this suborder being Daphniphyllaceae. The number recorded here for *Balanops*, $n = 21$, contributes little evidence on the relationships of the genus. Fagales have typically high base numbers of $x = 13$ (*Nothofagus*) and 12, but also $x = 8$ in

Carpinaceae (Raven, 1975). Notably, however, the isolated *Trigonobalanus* has $n = 22$ which may be significant in relation to Balanopaceae. Daphniphyllaceae have $n = 16$ (Fedorov, 1969).

CNEORACEAE

Neochamaelea pulverulentum (Vent.) Erdtm., $2n = 36$. Spain, Canary Islands, Tenerife, Adej, cult. Missouri Botanical Garden, *Goldblatt 4650* (MO).

Cneoraceae comprises two genera, the ditypic *Cneorum* of the western Mediterranean and Cuba and the monotypic *Neochamaelea* of the Canary Islands. The count for *Neochamaelea*, $2n = 36$, is the first report for the genus and is the same number as already recorded in the Mediterranean *Cneorum tricoccum*. (Goldblatt, 1976a).

LEDOCARPACEAE

Wendtia gracilis Meyer, $2n = 18$. Chile, Prov. Bio-Bio, Dept. La Laja, *Marticorena, Quevada & Rodíguez 984* (MO).

This is the first count for *Wendtia* and the second for the family, a segregate of Geraniaceae not always accorded familial status. The previous count in Ledocarpaceae was for *Balbisia verticillata* Cav., also $2n = 18$ (Diers, 1961).

MONTINIACEAE

Grevea eggelingii Milne-Redh., $2n = 24$. Tanzania, Mikumi National Park, *Wingfield s.n.* (ref. 'ole *Sayalel 1209* (DSM)).

This is the first chromosome count for *Grevea*, one of only two genera of Montiniaceae, an Afro-Madagascan family. The other genus, *Montinia*, has $n =$ ca. 34 (Goldblatt, 1976a). Chromosomes of *Grevea* are unusually large, and differ in this respect, as well as in number, from those of *Montinia* which has very small chromosomes. Cytological data are consistent with the comments of Metcalfe (in Milne-Redhead, 1955), based on anatomical characters, that the two genera are not particularly close allies.

Relationships of Montiniaceae are obscure, although the family has been associated with Onagraceae and Myrtales in a general way (Milne-Redhead, 1955). Anatomical data, specifically absence of intraxylary phloem in both genera, militate against this view. Other phylogenists have placed the family in or near Saxifragaceae (Cronquist, 1968, in Grossulariaceae; Takhtajan, 1969, in Saxifragales after Hydrangeaceae; Hutchinson, 1967, in Escalloniaceae; and Thorne, 1977, as Montinioideae).

Recently, Dahlgren et al. (1977) have shown that Montiniaceae (*Montinia* only examined) has iridoid compounds, making it unlikely that the family is related to Myrtales or Saxifragales, both of which lack iridoids. These workers proposed a relationship for the family close to Cornales, where Dahlgren (1975) places Escalloniaceae, Hydrangeaceae, and several other families sometimes placed in or near Saxifragales. Chromosome number of *Grevea* is alone of little help in assessing the affinities of Montiniaceae, but the number in *Grevea*, $n = 12$, is consistent with placement in Cornales, many families and genera of which have

base numbers at the paleotetraploid level (Goldblatt, 1978), including Escalloniaceae with $n = 12$, Cornaceae, $n = 13$ and 11, Curtisiaceae, $n = 13$.

MORACEAE

Trophis phillipinensis (Bur.) Corn., $2n = 28$. Indonesia, S. Celebes, 60 km from Macassar, *Meijer 10865* (MO).

The present count of $2n = 28$, a new generic record, is consistent with the known cytological pattern in Moraceae in which most genera have numbers in the range $2n = 28$–24 (Raven, 1975).

PEDALIACEAE

Uncarina grandidieri (Baill.) Stapf, $2n = 36$. Madagascar, southwest of Island, *Hardy s.n.* (PRE).

Counts in this small Indo-African family are in the range $2n = 32$–26 with one diploid record of $2n = 16$, suggesting $x = 8$ for the family. This first report for the arborescent *Uncarina* does not conform with the known pattern and suggests that $x = 9$ rather than 8 (Raven, 1975) may be basic for Pedaliaceae. *Uncarina* may well occupy a primitive position in the family, which comprises mostly perennial herbaceous forms.

ROSACEAE

Holodiscus discolor (Pursh) Max. var. *franciscana* (Rydb.) Jeps., $n = 18$. U.S.A., California, cult. Rancho Santa Ana Botanic Garden, (progeny of) Monterey Co., Carmel Valley, *Thorne 31461* (RSA).

This report is the first count for the genus *Holodiscus*. The haploid number of $n = 18$ is consistent with its position in subfamily Spiraeoideae ($x = 9$, Goldblatt, 1976b).

SABIACEAE

Meliosma panamensis Standl., $2n = 32$. Ecuador, Río Palenque, *Dodson & Gentry 6584* (MO).

The report of $2n = 32$ for this New World species of *Meliosma* corresponds with the several other counts for the genus, all $n = 16$ (Fedorov, 1969).

SCROPHULARIACEAE

Teedia lucida Rudolphi, $2n = 38$. South Africa, Cape, Worcester district, slopes of Jonas Kop, *Goldblatt s.n.* (no voucher).

Teedia is a small genus of only two species, confined to the Cape floristic region. Although it is somewhat isolated taxonomically within Scrophulariaceae, it has recently been linked to *Oftia*, also a South African genus (Dahlgren & Rao, 1971). Traditionally, though probably incorrectly, *Oftia* has been assigned to the predominantly Pacific Myoporaceae. Dahlgren and Rao's suggestion of a close relationship of *Oftia* with Scrophulariaceae and with *Teedia* in particular has been accepted by Dyer (1975) in a recent generic flora of southern Africa. Ad-

ditional support for this treatment has been provided by Niezgoda & Tomb (1975), who have shown that pollen of *Oftia* is unlike Myoporaceae and does resemble that found in some Scrophulariaceae. The present count for *Teedia* of $n = 19$ corresponds with the basic chromosome number in *Oftia*, also $x = 19$ (Goldblatt, 1976a). Myoporaceae, in contrast, have chromosome numbers based on $x = 9$ (Raven, 1975). Cytology thus provides additional evidence of a close relationship between *Teedia* and *Oftia*, particularly as $x = 19$ is an unusual number in Scrophulariaceae, having been recorded previously only in unrelated Australian members of the family (Briggs & Ehrendorfer, 1976).

TRIGONIACEAE

Trigonia cf. *virens* Macbr., $2n$ = ca. 20. Peru, Loreto, Río Yavari, *Gentry 20867* (MO).

The count for *Trigonia* obtained here is reported with some hesitation since there is doubt about its accuracy. The plants available for study were seedlings which grew poorly, producing very little root tip material for examination. I have decided to report the count since it is the first for Trigoniaceae, and as such is of interest. Trigoniaceae are a small family, generally accepted as belonging to Polygalales, and probably closely related to Malpighiaceae and Polygalaceae in both of which a fairly wide range of chromosome numbers has been found. The number in *Trigonia* is consistent with its position in Polygalales.

VOCHYSIACEAE

Vochysia lomatophylla Standl., $2n = 22$. Peru, Dept. Loreto, Río Tamishacu, *Gentry 25861* (MO).

This is the first chromosome count for this predominantly Neotropical family which consists mainly of canopy trees. The karyotype found here is distinctive. It consists of ten pairs of small chromosomes, ca. 2 μm in size, and acrocentric to submetacentric, and one large acrocentric pair, ca. 3 μm long with conspicuous, large satellites, some 2 μm long. Vochysiaceae is usually assigned to Polygalales, and is related to Trigoniaceae ($2n$ = ca. 20), Polygalaceae (cytologically diverse), and Malpighiaceae ($x = 6$: $2n = 24$, 22 and 20 frequent). The number found in *Vochysia lomatophylla* is consistent with numbers recorded in related families. Vochysiaceae is, however, a fairly large family of some 200 species in six genera, and more counts are required before further conclusions can be drawn about the taxonomic significance of the chromosome number found here, and the unusual, and most likely, derived karyotype.

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OBSERVATIONS OF CHROMOSOMES IN *LUDWIGIA* (ONAGRACEAE)[1]

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ABSTRACT

Chromosome numbers are reported for 38 of the 45 species of *Ludwigia* (Onagraceae) exclusive of sect. *Myrtocarpus* s. lat., based on a review of the literature and the study of 302 individuals from 283 naturally occurring populations from throughout the range of the genus. The basic chromosome number of the genus is $x = 8$, with no aneuploidy but extensive polyploidy. Among the 38 species of *Ludwigia* exclusive of sect. *Myrtocarpus* s. lat. that have been examined cytologically, there are 14 diploids ($n = 8$), 8 tetraploids ($n = 16$), 6 hexaploids ($n = 24$), 1 octoploid ($n = 32$), and 1 dodecaploid ($n = 48$), together with 4 species that include both tetraploids and hexaploids, 1 that includes both diploids and tetraploids, 1 that includes hexaploids and octoploids, and 1 that includes octoploids and decaploids. In the first two groups of species with intraspecific polyploidy, we believe that the tetraploids have given rise directly by the functioning of unreduced gametes to the populations with higher chromosome numbers. Multivalents have been observed in the genus only in single plants of tetraploid individuals of *L. octovalvis* and *L. pilosa*, and in *L. uruguayensis* ($n = 24, 40, 48$). There is no general correlation between breeding system and level of polyploidy in *Ludwigia*, as is manifest in several genera of annual Onagreae. *Ludwigia* seems less closely related to all other genera of Onagraceae than they are to one another. It originated at least 50 m.y. ago, probably in South America, where the family also is believed to have originated, but it reached the Northern Hemisphere also in the Eocene. The distinctive chromosome morphology of *Ludwigia*, in which the interphase nuclei are dotted with small chromocenters and the distal segments of the chromosomes are diffuse at mitotic mid-prophase, resembles that of Epilobieae, but seems clearly to have originated independently, like the other convergent morphological and physiological features in these two genera, from ancestors with more generalized chromosomes similar to those in *Fuchsia*, *Circaea*, and some species of *Lopezia*. Once the genome $x = 8$ had originated in the common ancestor of *Ludwigia*, polyploidy has been very frequent (at least two-thirds of the species are polyploid), and the genus has attained a very widespread distribution, particularly in the tropics and temperate North America, in the moist habitats where it occurs.

Ludwigia, a pantropical genus that is also well represented in temperate North America and has three endemic taxa in temperate Asia, includes some 80 species and is one of the largest genera of Onagraceae. It is very distinctive within this family and is the only genus of the tribe Jussiaeeae. Until the 1960s, the genera *Jussiaea* and *Oocarpon*, and sometimes also the genera *Isnardia* and *Ludwigiantha*, were conventionally segregated from *Ludwigia*, but more recent research and a better understanding of the phylogenetic relationships within the group has led to their grouping together within the genus *Ludwigia* (summary in Raven, 1963a), an alignment that now seems to have been adopted universally.

The chromosomes of *Ludwigia* sect. *Myrtocarpus* s. lat. will be treated by T. P. Ramamoorthy in his forthcoming revision of that group (Ramamoorthy, in prep.). Chromosome counts have been reported earlier for 6 species of sect. *Myrtocarpus* s. lat. out of a total of 32 (Gregory & Klein, 1960; Kurabayashi et al., 1962). In the

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remaining 16 sections of the genus (Raven, 1963a), there are some 45 species, of which chromosome numbers have been reported for what we regard as 16 species. In this paper we are reporting observations on 302 additional individuals representing a total of 283 populations of 38 species, including additional counts of all 16 species reported earlier (Tables 1–2). Of the seven remaining species, for which no chromosomal information is available, one is North American, two are Cuban endemics, and the remaining four are mainly South American, including the one uncounted section, sect. *Oocarpon*. We have also included all earlier reports in this paper with references, amounting to about 30 counts. Unless otherwise indicated, voucher specimens have been deposited at the Missouri Botanical Garden (MO). All counts were somatic except those indicated by "n = " numbers in parentheses following the citation of the vouchers. In all cases where the voucher citation is marked with an asterisk, the chromosome number determination was made in progeny grown from that collection, or from plants collected in the wild at the same time and grown on in the greenhouse. All collections prefixed by "R" were made by Raven, and all collections cited in parentheses are greenhouse vouchers.

The first report known to us of chromosomes in plants of the genus *Ludwigia* was that of Sinotô (1928), who reported $n = 8$ in the course of an investigation of pollen development in the taxon now known as *Ludwigia peploides* subsp. *stipulacea*. Chromosomes of another plant of this genus, of which the identity is not certain (see p. 870) were reported by Sharma & Sarkar (1956). They reported distinct differences in chromosome morphology and size within the genome, and that the size of the individual chromosomes ranged from 1–2.3 μm. In the diploid plant they investigated, they reported that some cells had $2n = 14$ and others $2n = 18$, and that even in cells with the normal chromosome number $2n = 16$, differences in chromosomes morphology could be observed. Such numerical differences have not, however, subsequently been found to be characteristic of individuals or populations in the genus, in which differentiation at the diploid level and polyploidy are the characteristic modes of differentiation.

Gregory & Klein (1960) reported chromosome numbers in 6 species of what is now regarded as *Ludwigia* sect. *Myrtocarpus* s. lat., and in what we now consider to be 12 additional species and 1 additional subspecies of the genus. They reported for the first time the widespread occurrence of polyploidy in the genus, but found no chromosomal heterozygosity or other irregularities in the samples they examined. They also mentioned differences in size between the chromosomes of different species. Later, in a study of mitotic chromosomes in Onagraceae, Kurabayashi et al. (1963) reported that the interphase nuclei of *Ludwigia* were dotted with small chromocenters which were more densely pycnotic than those of other Onagraceae, and that the distal segments of the chromosomes were diffuse at mitotic mid-prophase. The chromosomes were clearly heterogeneous with respect to their relative lengths and in the proportions of the proximal and distal regions, and they also differed conspicuously in size at metaphase, as reported earlier by Sharma & Sarkar (1956). Their diffuse distal regions were much more evident than the very short and inconspicuous ones of Epilobieae.

From 1962 onward, chromosome numbers were reported for what we would regard as five of the seven species of *Ludwigia* native to Asia (Chuang et al.,

TABLE 1. Chromosomes in *Ludwigia*, except sect. *Myrtocarpus* s. lat.

Section, Genus, Species	Chromosome Number
Sect. *Africana*	
L. jussiaeoides Desr.	$n = 32$
L. stenorraphe (Brenan) Hara subsp. *stenorraphe*	$n = 48$
Sect. *Brenania*	
L. brenanii Hara	$n = 24$
Sect. *Caryophylloidea*	
L. perennis L.	$n = 8$
Sect. *Cryptosperma*	
L. abyssinica A. Rich.	$n = 24$
Sect. *Dantia*	
L. arcuata Walt.	$n = 16$
L. brevipes (Long) E. H. Eames	$n = 24$
L. palustris (L.) Ell.	$n = 8$
L. repens Forst. (*L. natans* Ell.; Raven, 1965)	$n = 24$
L. spathulata Torr. & A. Gray	$n = 16$
Sect. *Fissendocarpa*	
L. hyssopifolia (G. Don) Exell	$n = 8$
Sect. *Ludwigia*	
L. alternifolia L.	$n = 8$
L. hirtella Raf.	$n = 8$
L. maritima Harper	$n = 8$
L. virgata Michx.	$n = 8$
Sect. *Macrocarpon*	
L. octovalvis (Jacq.) Raven	$n = 16, 24$
Sect. *Microcarpium*	
L. alata Ell.	$n = 16, 24$
L. curtisii Chapman	$n = 24, 32$
L. glandulosa Walt.	$n = 16$
L. linearis Walt.	$n = 8$
L. linifolia Poir.	$n = 8$
L. microcarpa Michx.	$n = 8$
L. pilosa Walt.	$n = 16$
L. polycarpa Short & Peter	$n = 16$
L. sphaerocarpa Ell.	$n = 16$
L. suffruticosa Walt.	$n = 16, 24$
Sect. *Miquelia*	
L. ovalis Miq.	$n = 16$
Sect. *Nematopyxis*	
L. prostrata Roxb.	$n = 8$
Sect. *Nipponia*	
L. epilobioides Maxim.	$n = 24$
Sect. *Oligospermum*	
L. adscendens (L.) Hara subsp. *adscendens*	$n = 16$
L. adscendens subsp. *diffusa* (Forsk.) Raven	$n = 16$
L. helminthorrhiza (Mart.) Hara	$n = 8$
L. hookeri (Michx.) Hara	$n = 8$
L. peploides (H.B.K.) Raven subsp. *glabrescens* (O. Kuntze) Raven	$n = 8, 16$
L. peploides subsp. *montevidensis* (Spreng.) Raven	$n = 8$
L. peploides subsp. *peploides*	$n = 8$

TABLE 1. Continued.

Section, Genus, Species	Chromosome Number
L. peploides subsp. *stipulacea* (Ohwi) Raven	$n = 8$
L. uruguayensis (Camb.) Hara	$n = 24, 40, 48$
Sect. *Prieurea*	
L. senegalensis (DC.) Troch.	$n = 8$
Sect. *Seminuda*	
L. affinis (DC.) Hara	$n = 32, 40$
L. africana (Brenan) Hara	$n = 24$
L. leptocarpa (Nutt.) Hara	$n = 16, 24$

1962; Sharma & Sharma, 1966; Mitra & Datta, 1967; Baquar, 1968; Pillay, 1970; Shetty & Subramanyam, 1971; Subramanyam, 1971; Sarkar et al., 1973), and the chromosome number for a sixth, *L. epilobioides,* was mentioned by Raven (1963a).

DISCUSSION OF RESULTS

SECT. *AFRICANA*

This ditypic African section consists of one monomorphic species, *Ludwigia jussiaeoides* ($n = 32$), and one extremely polymorphic one, *L. stenorraphe,* in which subsp. *stenorraphe* has $n = 48$. Chromosome counts of the other three subspecies of the latter would be highly desirable, and will probably suggest the taxonomic subdivision of this entity at the specific level (cf. Raven, 1963a).

SECT. *BRENANIA*

A very distinctive and local autogamous species, the hexaploid *Ludwigia brenanii* is known only from the Volta River drainage in southeastern Ghana.

SECT. *CARYOPHYLLOIDEA*

The diploid *Ludwigia perennis* is widespread in the Old World, highly autogamous, and morphologically quite uniform. The report by Pillay (1970) of $n = 16$ in this species may have been based on material of another species and needs to be confirmed. The material we counted from the same locality (Imphal) had $n = 8$ like all other populations of the species we have examined.

SECT. *CRYPTOSPERMA*

This monotypic section consists solely of the widespread, uniform, autogamous African endemic, *Ludwigia abyssinica,* which is hexaploid. As far as known, it is entirely hexaploid and has no close relatives.

SECT. *DANTIA*

This section will be treated in more detail by Schmidt & Raven (in prep.). Of the seven species listed by Raven (1963a), *Ludwigia* × *lacustris* E. H. Eames

is a sterile triploid hybrid, and *L. verticillata* Munz is a synonym of *L. inclinata* (L.f.) Raven (sect. *Myrtocarpus* s. lat.), a species in which the leaves on the lower, prostrate stems are verticillate, those on the upper flowering branches spirally arranged. Plants of *L. inclinata* in which the episepalous stamens are lacking occur intermixed with others in which they are present in the same populations, at least locally.

Of the remaining five species properly assigned to sect. *Dantia*, one is diploid, two are tetraploid, and two are hexaploid. All are autogamous except *L. arcuata*, in which the stigma is elevated above the anthers at anthesis (Schmidt, 1967).

SECT. *FISSENDOCARPA*

A morphologically uniform and widespread autogamous tropical weed without any close relatives, *Ludwigia hyssopifolia* is likewise apparently quite uniform cytologically, and entirely diploid.

SECT. *LUDWIGIA*

This section comprises four closely related and more or less interfertile species of which three are confined to the southeastern United States, and the fourth extends north to the midwestern states and southernmost Canada. All are diploid. Only *Ludwigia virgata* is regularly outcrossing, and in that species, the stigma is elevated well above the anthers at anthesis.

SECT. *MACROCARPON*

All species of sect. *Macrocarpon* except the widespread, weedy, autogamous *Ludwigia octovalvis*, long known as *Jussiaea suffruticosa* L., are restricted to the New World. They are being studied in detail, and their chromosome numbers will not be reported here, except to mention that among them are diploid species and two that are genetically self-incompatible.

Within *Ludwigia octovalvis* there are striking morphological differences that are reflected in a complex synonymy and in earlier efforts to divide the species into subspecies (Raven, 1963a). The kinds of densely pubescent, robust plants that we referred earlier to *L. octovalvis* subsp. *sessiliflora* (Mich.) Raven are especially distinctive in their extreme form, but they often grow side-by-side with less densely pubescent, more slender plants, the differences maintained by autogamy. In South America and Africa, the two sorts are nearly exclusively tetraploid ($n = 16$), whereas in Asia, the kinds of plants that exhibit parallel patterns of variation are almost all hexaploid ($n = 24$). To attempt to recognize the differences between these two sorts of plants in the formal taxonomy does not seem to accord with the biological realities of a remarkably complex species, and we now agree with Sreemadhavan (1966) that the species should not be subdivided formally (Raven, 1977).

The most distinctive race within the species, both morphologically and geographically, is that designated earlier as *Ludwigia octovalvis* subsp. *brevisepala* (Brenan) Raven (Raven, 1963a). Plants of this sort are abundant over most of Africa, where they are usually the only type of the species represented. In Mad-

agascar, southern and southeastern subtropical Africa, however, plants of the "*sessiliflora*-type," tetraploid like similar plants which are common in Brazil and elsewhere in South America, appear. Between the area occupied by such plants and the large, tropical African area of "*brevisepala*," plants like those characteristic of "subsp. *octovalvis*" in the rest of the world—i.e., relatively robust, large flowered, and less pubescent than "*sessiliflora*"—are frequent. It is possible, as suggested earlier, that the "*octovalvis*-type" plants in Africa might have originated following hybridization between "*brevisepala*-type" and "*sessiliflora*-type" plants; but autogamy is certainly the rule in all populations of this species worldwide. Taxonomically, it would be possible to continue to recognize "*brevisepala*-type" plants as a distinctive African subspecies, but to do so would be to leave a bewildering diversity of much more variable plants, widespread throughout the rest of the tropics and subtropics, grouped as subsp. *octovalvis*, since we are convinced that there is no practical way to continue to separate subsp. *sessiliflora* as a useful taxonomic entity.

With respect to chromosome number, most of the populations in the New World and all of those, as far as known, in Africa, are tetraploid ($n = 16$). The majority of populations in Asia, occupying an area extending to New Guinea and northern Australia, are hexaploid ($n = 24$). Plants from the Pacific Islands eastward to the New Hebrides and New Caledonia, in contrast, are tetraploid. Tetraploids also seem to occur locally in Asia, at least near Calcutta, India (Subramanyam, 1971; Sarkar et al., 1973) and near Chiengmai, Thailand. Reports of $n = 8$ and $2n = 16$ in this species from India (Mitra & Datta, 1967: 458, withdrawn by N. Datta in litt.; Sheriff & Mahalakshami, 1969, from Bangalore) seem to have resulted from confusion with other species, since later chromosome counts of other populations from the same areas have uniformly been $n = 24$. *Ludwigia octovalvis* is a very frequent weed of moist cultivated areas, readily carried about by commerce, and it seems to occur everywhere in the Pacific where there is human activity. The cytological pattern outlined here suggests that tetraploids from the New World have colonized both Africa and the islands of the Pacific, perhaps at least several times each, and that the widespread hexaploids of tropical Asia have originated there.

The two populations of *Ludwigia octovalvis* from the New World that had a gametic chromosome number of $n = 24$, one each from the Dominican Republic and from Venezuela, seem to be isolated cases. Hexaploid individuals in this species can doubtlessly arise directly from the tetraploids, as described earlier for *Gaura coccinea* Pursh (Raven & Gregory, 1972), and perhaps the hexaploids encountered represented only single populations, or even single individuals, that had originated in this way. This situation will be investigated further.

Of particular interest is the tetraploid individual from Clay Co., Florida, mentioned above. At meiotic metaphase I, it had 12 bivalents and 2 rings of 4 chromosomes, thus being one of the very few plants of *Ludwigia* in which meiotic irregularities have been found in a natural population.

Finally, it should be noted that populations of diploid ($n = 8$) individuals similar to *L. octovalvis* are frequent in Mexico, although they have not been found within the United States thus far. Examples of populations with $n = 8$ are as follows:

MEXICO. BAJA CALIFORNIA: Cape Region, *Thomas 7699**. GUERRERO: *Graham 427** (DS; *R67-L47*). JALISCO: *McVaugh 1659** (MICH; *R62054*). MICHOACÁN: *Porter 1391** (DS); ca. 17 mi E of Morelia, *Breedlove 7228* ($n = 8$).

Diploid populations of this sort can be distinguished only with difficulty from tetraploid populations of *Ludwigia octovalvis,* but they do have larger flowers and may well merit specific recognition. By Munz (1942) they were treated as *Jussiaea bonariensis* Mich. [=*L. bonariensis* (Mich.) Hara] when they were recognized as distinct from *J. suffruticosa* L. (=*L. octovalvis*), but they do not seem to be equivalent to the southern South American populations that include the type of that species. The much larger-flowered plants naturalized at Wilmington, New Hanover Co., North Carolina, on the other hand, are very distinct from any Mexican populations and may be the same as the South American ones, and have $n = 16$ (*R18731*). At any event, the Mexican diploid plants that resemble *L. octovalvis* must closely resemble the ancestral populations of this species, which might have originated essentially as an autotetraploid, with subsequent selection against quadrivalent formation. In any event, it is highly likely that the rings of chromosomes observed in the tetraploid Florida population of *L. octovalvis* mentioned above may reflect intergenomic chromosomal homology, and not the presence of reciprocal translocations within this plant.

SECT. *MICROCARPIUM*

Ludwigia sect. *Microcarpium* is a diverse but distinctive polyploid complex centering in the southeastern United States and extending into the islands of the Caribbean. Chromosome counts are now available for all taxa except the distinctive Cuban endemic *L. stricta* Wright ex Sauvalle, and, if it is distinct from *L. alata, L. lanceolata* Ell. The remaining ten species of the section consist of three diploids, *L. linearis, L. linifolia,* and *L. microcarpa*; four tetraploids, *L. glandulosa, L. polycarpa, L. pilosa,* and *L. sphaerocarpa,* of which the latter two are very closely related and appear to replace one another geographically and to intergrade in nature; and three species that have more than one chromosome number—*L. alata* ($n = 16, 24$); *L. curtisii* ($n = 24, 32$); and *L. suffruticosa* ($n = 16, 24$). In both *L. alata* and *L. suffruticosa,* it is likely that the hexaploids arose directly from the tetraploids by the functioning of an unreduced gamete, as postulated above for populations of *L. octovalvis* (sect. *Macrocarpon*) in the Dominican Republic and in Venezuela. The situation in *L. curtisii* is apparently more complex, with the diploid *L. microcarpa* evidently having played a role in the evolution of the polyploid complex. Within this group, the differentiating characteristics ascribed to *L. spathulifolia* and to *L. simpsonii* certainly are not correlated with the differences in chromosome number and, furthermore, are subject to environmental modification so that capsule shape and size and leaf shape, which may appear distinctive in the field, tend to converge in the experimental garden.

Within the section, *Ludwigia linifolia* ($n = 8$), *L. glandulosa* ($n = 16$), and *L. polycarpa* ($n = 16$) seem related, as do *L. stricta, L. microcarpa* ($n = 8$) and *L. curtisii* ($n = 24, 32$); in turn, there might well be a relationship between these two groups. Species in which the apex of the ovary and nectaries are yellow and

attractive to insects, even though the flowers lack petals, are *L. pilosa* ($n = 16$) and *L. sphaerocarpa* ($n = 16$), which as we have mentioned are very closely related and possibly even best regarded as conspecific, and *L. alata* ($n = 16, 24$), *L. lanceolata* (if it is distinct), and *L. suffruticosa* ($n = 16, 24$). There may very well be a relationship between the first two species and the last three, even though the first two shed their pollen in tetrads, the last two singly (Raven, 1963a). Petals occur in species of sect. *Microcarpium* only in *L. linifolia* ($n = 8$), *L. stricta*, and *L. linearis* ($n = 8$); recently Eyde (1978) has shown that the last-mentioned species differs from all others assigned to the section in having the sporogenous tissue in its anthers divided into packets by sterile tissue. Despite this characteristic, it resembles *L. glandulosa* ($n = 16$) morphologically and might be directly related to it. Biosystematic investigations to clarify the relationships of the species of this complex further are underway.

The collection of *Ludwigia pilosa* from Colleton Co., South Carolina, mentioned above, formed 14 bivalents and a ring of 4 chromosomes at meiotic metaphase I. As in the individual of *L. octovalvis* discussed above, it is presumed that the ring of chromosomes was formed because of homology between the two genomes combined in this species, and not because of the presence of a reciprocal translocation, but the situation should be investigated further.

SECT. *MIQUELIA*

Ludwigia ovalis, a very distinctive East Asian species, combines the prostrate habit of sect. *Dantia*, the spirally arranged leaves of sect. *Microcarpium*, and its own very specialized seeds. It certainly finds its closest relatives in these primarily North American sections of temperate to subtropical regions. As far as known, it is tetraploid.

SECT. *NEMATOPYXIS*

Ludwigia prostrata is a highly autogamous, diploid species without any close relatives.

SECT. *NIPPONIA*

As reported earlier (Raven, 1963a), both subspecies of *Ludwigia epilobioides*, an autogamous, distinctive East Asian species, are hexaploid ($n = 24$).

SECT. *OLIGOSPERMUM*

The chromosome numbers reported here, which include all species of the section except for the Cuban endemic *Ludwigia peduncularis* (Wright ex Gris.) Gómez, indicate that this very widespread group is a polyploid complex. Owing to the complex pattern of intergradation in Madagascar (Raven, 1963a), and to the demonstrated tetraploidy of *L. adscendens* subsp. *adscendens*, we are now tentatively following Raynal (1966) in part in treating the entities we earlier distinguished as *L. stolonifera* and *L. adscendens* as subspecies of an Old World tetraploid species. This species and the New World, white-flowered *L. helmin-*

thorrhiza ($n = 8$) are the only members of the section in which pneumatophores are consistently formed on the floating stems; all members of the group form such pneumatophores from the underground parts. Of the taxa of this section, only *L. helminthorrhiza* and *L. adscendens* subsp. *adscendens* have white petals, instead of the more frequent bright yellow ones.

Contrary to Raynal (1966), we still prefer to maintain the diploid *Ludwigia peploides* as a distinct species, even though it is represented both north and south of the tropical area of *L. adscendens* subsp. *adscendens* in Asia and Australia. An experimental hybrid between the strain of *L. peploides* subsp. *glabrescens* reported above from Arkansas and that of *L. peploides* subsp. *stipulacea* from Kanagawa Prefecture, Japan, which was grown in the greenhouse formed 8 bivalents at meiotic metaphase I and was fully fertile as to both pollen and seed set. Presumably the tetraploid plant of *L. peploides* subsp. *glabrescens* reported above from Mississippi had had a local origin. The chromosome number $2n = 24$ reported by Chuang et al. (1962) for *L. peploides* subsp. *stipulacea* from Taiwan is almost certainly based upon a spontaneously occurring triploid individual with one unreduced gamete, and some of the elements in their drawing resemble trivalents. The chromosome number $n = 8$ is presumably characteristic of this entity in Taiwan as elsewhere in its wide range. More puzzling is the report of Sharma & Sarkar (1956) of a diploid individual of *L. adscendens* subsp. *adscendens* from India, but the report needs to be confirmed. The authors stated that the flowers of the plant they examined were either yellow or white, strongly suggesting that other species, perhaps the diploid *L. perennis*, may have been involved.

Otherwise, it appears that there may be two distinct elements within *Ludwigia uruguayensis*, one with $n = 24$ (and $n = 48$) and the other with $n = 40$. Multivalents are frequent in both, and they might well be separable taxonomically following further study. Based on a single count, *L. hookeri* seems to be diploid, whereas the Cuban *L. peduncularis* is probably a high polyploid, judged from its 5–8-pored pollen.

SECT. *PRIEUREA*

As discussed earlier (Raynal, 1966; Raven, 1978), the segregation of taxonomic units within this vegetatively plastic section appears indefensible in view of the behavior of the plants observed under different conditions in the experimental garden. We therefore regard this section as comprising a single, diploid species. The species forms a number of distinctive biotypes which are presumably reinforced by its almost total autogamy. It has no apparent relatives within the genus.

SECT. *SEMINUDA*

Ludwigia sect. *Seminuda* constitutes a polyploid complex in which no diploids have yet been discovered. Only the New World populations of *L. leptocarpa* are known to be only tetraploid, with all other strains examined hexaploid, octoploid, or decaploid. Whether the patterns implied by the results reported here will hold true awaits further chromosome number determinations, especially within *L. affinis* and the South American and African populations of *L. leptocarpa*.

General Discussion

Chromosome numbers are now available for 38 of the 45 species of *Ludwigia*, excluding sect. *Myrtocarpus* s. lat., and for 16 of the 17 sections of the genus, including all except the monotypic sect. *Oocarpon*. All 25 species of *Ludwigia* that occur in the Old World have now been studied cytologically. Within the group of 38 species for which chromosome numbers are available, there are 14 diploids (n = 8), 8 tetraploids (n = 16), 6 hexaploids (n = 24), 1 octoploid (n = 32), and 1 dodecaploid (n = 48), as well as 4 species that include both tetraploids and hexaploids, 1 that includes diploids and tetraploids, 1 that includes hexaploids and octoploids, and 1 that includes octoploids and decaploids. In the first two classes of intraspecific polyploidy, we believe that the tetraploids have given rise to the hexaploids (by the functioning of an unreduced gamete) and octoploids directly. The latter two cases, involving *L. curtisii* and *L. affinis*, require further investigation. Polyploidy is well scattered throughout the different sections, and two—*Africana* and *Seminuda*—seem to be exclusively polyploid.

As reported above, multivalents were observed at meiotic meiosis in single plants of tetraploid individuals of *Ludwigia octovalvis* and *L. pilosa*, and were frequent in plants of *L. uruguayensis* with the three chromosome numbers encountered in that complex species, n = 24, 40, and 48. We consider all of these multivalents to be associated with intergenomic homology, and there is no unequivocal evidence for the presence of reciprocal translocations in *Ludwigia*, either in naturally occurring plants or in hybrids. No evidence of inversions has been encountered either.

In the 45 species of *Ludwigia* that have not traditionally been included in sect. *Myrtocarpus* s. lat., there appears to be no general correlation between breeding system and polyploidy. Approximately 29 of the species are normally self-pollinating, including representatives of every section except *Africana* (2 species); of the 14 known diploids, 7 are mainly outcrossing. The only modally outcrossing species in sect. *Dantia* is a tetraploid; the 7 species of sect. *Oligospermum* are outcrossing as a group (except perhaps for *L. hookeri*), regardless of the level of polyploidy; and the ditypic African polyploid sect. *Africana* is entirely polyploid and outcrossing. Moreover, there is no apparent correlation between the extent of vegetative reproduction and polyploidy.

In terms of its relationships within the family, *Ludwigia* now seems to represent a distinct branch from the common ancestor of the family, with all other living genera on the other branch (Broekens, 1924; Johansen, 1929; Melchior, 1964; Takhtajan, 1959, 1966; Eyde & Morgan, 1973; Eyde, 1977, 1978, pers. comm.). In cladistic terms it is the "sister group" of all other Onagraceae. This relationship implies that the distinctive chromosomes of *Ludwigia*, which are specialized both in number and in morphology (Kurabayashi et al., 1962), were derived from an ancestor common to *Ludwigia* on the one hand and all other members of the family on the other. From this common ancestor, which almost certainly had a gametic chromosome number of n = 11 and generalized chromosomes that did not contract unevenly or remain dotted with obvious chromocenters in interphase like those of *Ludwigia* (Kurabayashi et al., 1962), *Ludwigia*, with x = 8 and highly specialized chromosomes, was derived. This event seems almost certainly to have taken place in South America (Skvarla et al., 1978), the

center for the evolution and radiation of *Ludwigia* (Raven, 1967; Raven & Axelrod, 1974). Both the hypothetical common ancestor of the family and the original species of *Ludwigia* seem to have had 4+-mery (Eyde, 1978), whereas 4+-mery evidently was characteristic of the common ancestor of all other Onagraceae, and interxylary phloem clearly originated in the family within this second major line (Carlquist, 1975).

Although diverse enough, particularly in the characteristics of the seeds, capsules, and androecia, to be divided into at least 17 sections (Raven, 1963a), *Ludwigia* is in other respects, such as pollen (Skvarla et al., 1975, 1976), one of the most homogeneous genera of Onagraceae. Its pollen is known from the Eocene of South America (Gonzáles G., 1967), British Columbia (Rouse, 1962), and the Soviet Far East (Bratseva, 1969), indicating not only a considerable antiquity for the genus, but also an early dispersal to North America and the rest of the world (Raven & Axelrod, 1974). Within *Ludwigia,* the 5(–6)-merous line that includes sect. *Oligospermum* and the closely related sect. *Oocarpon* seems to have diverged from the extinct common ancestor of sect. *Myrtocarpus* s. lat. before the stabilization of 4-mery in the genus (Eyde, 1977). Since the pollen is shed singly in sects. *Oligospermum* and *Oocarpon,* and in tetrads in all other outcrossing species of *Ludwigia,* this also implies that the common ancestor of *Ludwigia* shed its pollen singly, and that the habit of shedding the pollen in tetrads originated separately in *Ludwigia* and in the Epilobieae, as earlier hypothesized (Skvarla et al., 1975). The evolutionary relationships outlined here also suggest that the specialized chromosome morphology of *Ludwigia* and of Epilobieae, which is somewhat similar, and the paludal habit of these two groups, likewise evolved separately. Such a conclusion is in accordance with evidence derived independently from Epilobieae, which suggests that the common ancestor of that tribe, which seems clearly to have originated in the Northern Hemisphere and almost certainly in western North America, occurred in xeric habitats (Raven, 1976). Epilobieae, Onagreae, and Lopezieae, the three tribes in which interxylary phloem occurs (Carlquist, 1975), all seem to have originated in western and southern North America and might conceivably even have a common ancestor with *Fuchsia,* which is mainly South American, and *Circaea,* widespread in temperate forests of the Northern Hemisphere. *Hauya,* which lacks interxylary phloem (Carlquist, 1975), shares some similarities with Onagreae and might represent an offshoot of the line leading to that large and diverse tribe, unless convergent evolution was involved.

Ludwigia, then, has been a successful genus of wet habitats in the tropics for at least 50 million years, with several well-developed temperate offshoots, particularly in North America but also in Asia. Once the chromosome number of this genus stabilized at $n = 8$, there have been no further aneuploid changes, but polyploidy has been frequent and an important part of the evolutionary strategy in most parts of the genus. Unlike the situation in Onagreae, polyploidy in *Ludwigia* does not appear to be correlated closely with autogamy, and, for the present, one can only speculate about the reasons for this major evolutionary difference, which presumably reflects some aspect of the adaptive systems of the two groups. It may be pointed out, however, that the autogamous polyploids of Onagreae are almost invariably annuals, with their presumed emphasis on *r*-selected

exploitation of highly specific marginal habitats in which the production of a very high frequency of precisely adapted individuals may be at a higher premium than in the wet, and thus perpetually open, habitats of *Ludwigia* species.

TABLE 2. Chromosomes in *Ludwigia*, except sect. *Myrtocarpus* s. lat.

Sect. *Africana*

Ludwigia jussiaeoides Desr. ($n = 32$).

MOZAMBIQUE. Cabo Delgado Dist., *Torre & Paiva 1165*[a] (LISC, *R67-L14*).

Ludwigia stenorraphe (Brenan) Hara subsp. *stenorraphe* ($n = 48$).

GHANA. S of Attebubu, *Morton A465**. TOGO. Nr. Defale, *Morton A4426** (MO; *R18109*). ZAMBIA. Nr. Chingola, *Fanshawe in 1968**; Ndola, *Mutimushi 748** (K, *R67-L11*); 55 km N of Kasempa, *Robinson 5547** (K, *R67-L12*).

Sect. *Brenania*

Ludwigia brenanii Hara ($n = 24$).

GHANA. *Hall 899** (*R67-L9*); Kete Krachi, Volta R., *Hall VBS022** (*R19702*).

Sect. *Caryophylloidea*

Ludwigia perennis L. ($n = 8$).

BANGLADESH. Rangamati, Chittagong Hill tracts, Bangladesh, *Baquar in 1967* ($n = 8$; Baquar, 1968, as *L. parviflora*). INDIA. Gauhati, *Santapau 35508** (*R19094*); Bombay, *Patel** (*R18066*, DS); Imphal, Manipur, progeny, *R17440*; Hooghly, Kamarkundu, West Bengal, India, *Shetty 82* ($n = 8$; Shetty & Subramanyam, 1971). PHILIPPINES. Mt. Makiling and vicinity, Laguna Prov., *Stern 2340* ($n = 8$). ZAMBIA. Mazubuka Dist., *van Rensburg 1907* (SRGH, *R32*).

Sect. *Cryptosperma*

Ludwigia abyssinica A. Rich. ($n = 24$).

ETHIOPIA. Wallaga Prov., *Mooney 6793** (S, *R61-3*; also $n = 24$). NIGERIA. Ibadan, Oyo Prov., *Morton in 1961* (R17122, R18067)*. SIERRA LEONE. Nr. Fintonia, *Morton & Gledhill S1486**. ZAÏRE. Nr. Kinzao Vuete, *Compère 256** (BR, *R61-13*).

Sect. *Dantia*

Ludwigia arcuata Walt. ($n = 16$).

UNITED STATES. Florida: Hillsborough Co., Tampa, *Lakela 24805** (also $n = 16$); nr. Tallahassee, Leon Co., *Godfrey 62861**; 2 mi S of Oakland, Orange Co., *Godfrey 57332** (RSA; $n = 16$, Gregory & Klein, 1960).

Ludwigia brevipes (Long) E. H. Eames ($n = 24$).

UNITED STATES. North Carolina: Byrds Mill Pond, S of Bunnlevel, Harnett Co., *Ornduff 6465** (*R18101*, also $n = 24$); Holts Lake, 4 mi SW of Smithfield, Johnston Co., *Ornduff 6463** (*R18104*, also $n = 24$); 3.2 mi N of Lumberton, Robeson Co., *Lloyd 1030** (also $n = 24$).

Ludwigia palustris (L.) Ell. ($n = 8$)

COSTA RICA. Tres Ríos, Cartago Prov., *R in 1967**. FRANCE. Sologne, *Schotsman* (P; Schotsman, 1970). PORTUGAL. Santana Ferreira, Matas de Foja, *Queirós 1720, 6038* (COI; Queirós, 1976). UNITED KINGDOM. Hatchet Pond, near Beaulieu, Hampshire, England, *R16321* ($n = 8$). UNITED STATES. Arkansas: Terre Noir Creek bottoms, Clark Co., *Demaree 48955**; 10 mi W of Hot Springs, Garland Co., *Munz & Gregory 23502* (RSA; Gregory & Klein, 1960, as var. *americana*). California: Santa Cruz Co., *V. Hesse in 1961** (*R17943, 17944*; $n = 8$); Sonoma Co., *Rubtzoff 4778** (*R18068*; $n = 8$). North Carolina: 8 mi N of Fayetteville, Cumberland Co., *Lloyd 1025**. 5.1 mi S of Lillington, Harnett Co., *Lloyd 1021**. 3.2 mi N of Lumberton, Robeson Co., *Lloyd 1029**. Oklahoma: Adair Co., *R20420**. Texas: 12 mi W of Beaumont, Jefferson Co., *Munz & Gregory 23459* (RSA; $n = 8$; as var. *nana*); Liberty Co., *R19649**, *19650**. Virginia: *Lloyd** (*R18089*); Isle of Wight Co., *Lloyd 712** ($n = 8$).

Ludwigia repens Forst. (*L. natans* Ell.; Raven, 1965) ($n = 24$).

MEXICO. Nuevo León: Río Ramos, between Monterrey and Linares, *Hotchkiss & Tindale** (*R19634*). UNITED STATES. California: San Bernardino Co., *R16681* ($n = 24$). Florida: 37 mi SE of Perry, Dixie Co., *Munz & Gregory 23467* (RSA; $n = 24$; as *L. natans* var. *natans*); Orange Co., *Lakela 24902** (*R17933*, $n = 24$), *24903* in part* (*R17932*). Texas: Fort Bend Co., *R19402* ($n = 24$).

TABLE 2. Continued.

Ludwigia spathulata Torr. & A. Gray ($n = 16$).

UNITED STATES. Florida: Ca. 2 mi N of Woodville, Leon Co., *Godfrey 62880** (DS, FSU, NY; also $n = 16$).

Sect. *Fissendocarpa*

Ludwigia hyssopifolia (G. Don) Exell ($n = 8$).

BORNEO. Kuching, *Hsuan Keng** (*R65-69*). BRAZIL. Santana, Terr. Amapa, *Pires et al. 51108** (*R20185*). CHINA. Sah-Pai, Taipeh Co., Taiwan, *Chuang et al. 4321** ($n = 8$, *R18065*). INDIA. Bombay, *Patel** ($n = 8$, *R18066*); Cuttack, 300 mi N of Waltair, *P. N. Rao** (*R20188*); Bangalore, *Satyanarayanachar** (*R74-149*); Hooghly, Kamarkundu, W. Bengal, *Shetty 86* ($n = 8$; Shetty & Subramanyam, 1971). NEPAL. Ghorwa, ca. 300 m elev., below Ilam, *Hara & Kurosawa in 1963**. PERU. Dept. Loreto, *Mathias 3496** (RSA, *R62034*); Prov. Quispicanchis, *Vargas 15356** (US). PHILIPPINES. Davao City, *Pancho in 1963** (*RG65-68*); Mt. Makeling and vicinity, *Stern 2217* ($n = 8$; MO). EL SALVADOR. Dept. San Salvador, *Porter 1289** (GH, *RG65-26*). SAMOA. Apia, *Carlquist** (*RG65-67*). SIERRA LEONE. *Morton SL1219**. SURINAM. 20 km N of airstrip, Kabalebo R., *Florschütz & Maas 2562* (U; Gadella & Kliphuis, 1968). ZAÏRE. *Wagemans 2299** ($n = 8$; BR).

Sect. *Ludwigia*

Ludwigia alternifolia L. ($n = 8$).

UNITED STATES. Arkansas: Garland Co., *Demaree 40523* ($n = 8$, Gregory & Klein, 1960, as var. *pubescens*). Florida: Jefferson Co., *R18615* ($n = 8$). Georgia: Jasper Co., *R18706**; Meriwether Co., *R18559* ($n = 8$). Iowa: Johnson Co., *P. Sorensen in 1961** (*R20231*). Kansas: Reno Co., *Anderson 2811** (DS; *R20229*). Massachusetts: Middlesex Co., *Solbrig** (*R20237*). Mississippi: Jackson Co., *R18584* ($n = 8$); Lauderdale Co., *R18565* ($n = 8$); Perry Co., *R18574* ($n = 8$). North Carolina: Orange Co., *Totten** (*R20227, R20232*); Sampson Co., *Lloyd 1117* ($n = 8$). Rhode Island: Washington Co., *R16517* ($n = 8$). South Carolina: Beaufort Co., *Gregory 533* ($n = 8$); Oconee Co., *Ornduff in 1962** (*R18053*).

Ludwigia hirtella Raf. ($n = 8$).

UNITED STATES. Florida: Baker Co., *R18695* ($n = 8$). Georgia: Colquitt Co., *Godfrey 67460**; Grady Co., *Godfrey 63223**.

Ludwigia maritima Harper ($n = 8$).

UNITED STATES. Alabama: Baldwin Co., *R18589**. Florida: Jefferson Co. *R18614* ($n = 8$); Nassau Co., *R18700**; Orange Co., *Godfrey 57354** ($n = 8$; RSA, Gregory & Klein, 1960).

Ludwigia virgata Michx. ($n = 8$).

UNITED STATES. Florida: Baker Co., *R19654**; Wakulla Co., *R18606* ($n = 8$). Georgia: Grady Co., *Godfrey 63222** (*R19728*). North Carolina: New Hanover Co., *Ahles** (*R65-41*).

Sect. *Macrocarpon*

Ludwigia octovalvis (Jacq.) Raven. Plants with $n = 16$.

BRAZIL. Santana, Terr. Amapá, *Pires et al. 51109**; Itajai, Est. Santa Catarina, *Sehnem** ($n = 8$; *R18097*), *Dietrich** (*R74-174*); Est. São Paulo, *Ormond 121** (*R67-L6*), *128** (*R67-L4*). COSTA RICA. Prov. Puntarenas, *R21982* ($n = 16$), *Sullivan 382** (DS, *R67-L46*); Prov. Cartago, *Dressler in 1965** (*R65-183*). DOMINICA. *Ernst 1328** (DS; *R67-L16*). FIJI. *Parham 14342* (DS; *R67-L49*), *14343* (DS; *R67-L48*); above Suva, Viti Levu, *Carlquist** (*R20191*). GHANA. *Morton A4438** (*R18084*); Legon, *Morton in 1961** ($n = 16$; *R16866*). INDIA. West Bengal, Garia (Subramanyam, 1971); Indian Botanical Garden, Calcutta (*N. Datta B, C*, 4 plants, meiotic and somatic determinations; Sarkar et al., 1973); Andul, Howrah Distr., *N. Datta A*; Kolaghat, Midnapur Distr., *N. Datta D*. MEXICO. 20 mi S of La Trinitaria, Chiapas, *Breedlove 10039**; 4.5 mi NE of Bochil, Chiapas, *Breedlove 10191**; 5 mi S of Jitotol, Chiapas, *Breedlove 11955* ($n = 16$); 8 mi E of Cintalapa, Chiapas, *Breedlove 10308**; 9 mi SW of Valle Nacional, Oaxaca, *Breedlove 8041**; 3 km N of Valle Nacional, *Stone 1832** (DS); Veracruz, *Romero 77** (DS). MOZAMBIQUE. Malema, Mocambique Dist., *R19635**. NEW CALEDONIA. Tontoroita, *Carlquist in 1962**. NEW HEBRIDES. Espíritu Santo, *Carlquist** (*RG65-50*). PANAMA. Juan Mina, *Dressler in 1962**. PERU. Nr. Iquitos, *Mathias 3533** (LA, RSA, *R18098*; $n = 16$, *R62036*), *3953**, *Dressler** (*R20235*), *Dressler** (*R20183*); Muyuy, *Dressler** (*R20236*). RHODESIA. *Methuen 297** (PRE; *R65-192*). SAMOA. Saleimoa to Matauta, *Carlquist** (*R20669*). SIERRA LEONE. *Morton SL1217** (K; *R20189*). SOUTH AFRICA. Ca. 52 mi W of Louis Trichardt, Transvaal, *Schleiben 7478** (G; *R16620*). TANZANIA. Mpanda Dist., *Harley 9449** (K; *R in 1963*). THAILAND. Chiengmai, *Sorensen et al. 5328** (C), *5329* (C). TOGO. Nr. Defale, *Morton A4438** ($n = 16$; *R62018*). TRINIDAD.

TABLE 2. Continued.

Aripo Savanna, *Jermy 3183** (BM), *3187** (BM), *H. G. Baker in 1962** (*R20269*). UNITED STATES. Florida: Prairie Lake, *Schallert 16221** ($n = 16$; S; *R16619*); Broward Co., *Sternberg in 1974** (2 collections); Clay Co., *R18687* (see below); Collier Co., *R18670* ($n = 16$), *Munz & Gregory 23475* ($n = 16$; RSA; Gregory & Klein, 1960, as *Jussiaea suffruticosa* var. *ligustrifolia*); Highlands Co., *R18682* ($n = 16$); Hillsborough Co., *R18646* ($n = 16$), *R18647* ($n = 16$). Hawaii: Oahu, *Gillett in 1964** (DS). Mississippi: Jackson Co., *R18582* ($n = 16$). VENEZUELA. Nr. Samariapo, Amazonas, *Gentry 14568*, 14608**; Rancho Grande, *Medina in 1964** (*R65-187*); Caucagua, *Medina** (*R20672*). ZAÏRE. Nr. Kinzao Vuete, *Compère 256* (BR; *R16669*).

Ludwigia octovalvis. Plants with $n = 24$.

AUSTRALIA. Northern Territory, *Nelson 287** (DS). CHINA. Taichung Co., Taiwan, *De Vol et al. 433** (*R20270*), *Chuang & Lin T1C4780* ($n = 24$; Chuang et al., 1962), *Chuang T1C3905* ($n = 24$; Chuang et al., 1962), Sah-Pai, Taipeh Co., Taiwan, *Chuang et al. 4318** (*R18130*). DOMINICAN REPUBLIC. Nr. Santiago de los Caballeros, *Jiménez in 1962** (*R65-63*). INDIA. Bangalore, *Satyanarayanachar** (*R74-147*); 150 mi S of Waltair, *P.N. Rao** (*R18133*); Gauhati, *Santapau 34797** (*R19651*); S Kamrup, Assam, *Srinivasan 39183** (*R67-L18*). JAPAN. Amami-Oshima, Ryukyu Isls., *S. Hatusima** (R20184). MALAYA. Nr. Kuala Lumpur, Selangor, *Kassim** (*R67-L21*). NEW GUINEA. Wantipi Village, Sepik Dist., *Darbyshire & Hoogland 8303** (K; *R62037*); Bulolo, *Jermy in 1964**, Finisterres, *Jermy in 1964** (*R65-96*); Mengea, 3,600 ft elev., *Jermy in 1964** (*R65-98*); Butnari to Wonenara, Eastern Highlands, 6,000 ft elev., *Carlquist in 1963** (*R65-60*); Aitape Subdistrict, Sepik Dist., *Darbyshire & Hoogland 8303**. SINGAPORE. Botanical Garden, *R65-55**. VENEZUELA. Jardín Botánico, Caracas, *Medina in 1964**.

Sect. *Microcarpium*

Ludwigia alata Ell. Plants with $n = 16$.

UNITED STATES. Florida: Collier Co., *R18672**; Highlands Co., *R18684* ($n = 16$), *R18681* ($n = 16$), *R17927**.

Ludwigia alata. Plants with $n = 24$.

UNITED STATES. Florida: Wakulla Co., *R18608* ($n = 24$). Georgia: Charlton Co., nr. Cravens Hammock, *R in 1974**. South Carolina: Horry Co., *R18719* ($n = 24$).

Ludwigia curtisii Chapman (including *L. simpsonii* Chapman and *L. spathulifolia* Small). Plants with $n = 24$.

UNITED STATES. Florida: Collier Co., *Munz & Gregory 23476* ($n = 24$; Gregory & Klein, 1960); Hillsborough Co., *R18649** (also $n = 24$); Martin Co., *Munz & Gregory 23481* (RSA; Gregory & Klein, 1960, as *L. simpsonii*); Sarasota Co., *R18640* ($n = 24$).

Ludwigia curtisii. Plants with $n = 32$.

UNITED STATES. Florida: Dade Co., *Godfrey 63396**; Monroe Co., *Godfrey 63519**; Sarasota Co., *R18662**.

Ludwigia glandulosa Walt. ($n = 16$).

UNITED STATES. Alabama: Macon Co., *R18562* ($n = 16$). Arkansas: *Demaree 46645** (*R65-42*). Florida: Jefferson Co., *R18617* ($n = 16$); Leon Co., *Godfrey** ($n = 16$; Gregory & Klein, 1960); Madison Co., *R18628* ($n = 16$). Louisiana: St. Tammany Parish, *R18577* ($n = 16$); Tammany Parish, *R18576* ($n = 16$). Mississippi: Jones Co., *R18569* ($n = 16$). Texas: Fort Bend Co., *R19398* ($n = 16$), *R19405* ($n = 16$); Liberty Co., *R19427* ($n = 16$).

Ludwigia linearis Walt. ($n = 8$).

UNITED STATES. Alabama: Baldwin Co., *R18590* ($n = 8$). Arkansas: *Demaree 46998** (*R65-43*). Florida: Madison Co., *R18627* ($n = 8$). Louisiana: St. Tammany Parish, *R18579* ($n = 8$). Mississippi: Jackson Co., *R18585* ($n = 8$). North Carolina: Cumberland Co., *Lloyd 1026* ($n = 8$); Johnston Co., *Lloyd 1121* ($n = 8$). South Carolina: Horry Co., *R18721* ($n = 8$).

Ludwigia linifolia Poir. ($n = 8$).

UNITED STATES. Florida: Okaloosa Co., *R18593* ($n = 8$). Mississippi: Hancock Co., *R18581* ($n = 8$); Jackson Co., *Demaree 37879** (Kurabayashi et al., 1962; also $n = 8$; Gregory & Klein, 1960).

Ludwigia microcarpa Michx. ($n = 8$).

UNITED STATES. Florida: Clay Co., *R18692* ($n = 8$, also in progeny); Hillsborough Co., *R18641* ($n = 8$); Wakulla Co., *R18601* ($n = 8$), *R18610* ($n = 8$).

TABLE 2. Continued.

Ludwigia pilosa Walt. ($n = 16$).

UNITED STATES. Florida: Clay Co., *R19690* ($n = 16$); Highlands Co., *R18683* ($n = 16$); Leon Co., *Kral in 1963** (*R65-44*); Madison Co., *R18625* ($n = 16$); Walton Co., *R18594* ($n = 16$). Georgia: Camden Co., *R18701* ($n = 16$). Mississippi: Hancock Co., *R18580* ($n = 16$); Jackson Co., *R18583* ($n = 16$); Jones Co., *R18568* ($n = 16$). South Carolina: Colleton Co., *R18717* ($n = 16$; see below); Jasper Co., *R18712* ($n = 16$).

Ludwigia polycarpa Short & Peter ($n = 16$).

UNITED STATES. Massachusetts: Middlesex Co., *R16514* ($n = 16$). Michigan: Washtenaw Co., *R16523* ($n = 16$).

Ludwigia sphaerocarpa Ell. ($n = 16$).

UNITED STATES. Without definite locality, *Monoson 55** (RSA; Gregory & Klein, 1960). Florida: Clay Co., *R18680* ($n = 16$; intermediate to *L. pilosa*); Columbia Co., *R18634* ($n = 16$); Madison Co., *R18626* ($n = 16$), *R18630* ($n = 16$); Taylor Co., *R18620* ($n = 16$). Indiana: Starke Co., *R16525* ($n = 16$; = "var. *deamii* Fern. & Grisc."). Massachusetts: Plymouth Co., *R16516* ($n = 16$). South Carolina: Beaufort Co., *R18716* ($n = 16$; intermediate to *L. pilosa*); Colleton Co., *R18718* ($n = 16$).

Ludwigia suffruticosa Walt. Plants with $n = 16$.

UNITED STATES. Florida: Glades Co., *R18678**; Lake Co., *R18637* ($n = 16$); Leon Co., *R18585* ($n = 16$); Polk Co., *Lakela 24806** (*R19704*); Taylor Co., *R18619* ($n = 16$).

Ludwigia suffruticosa. Plant with $n = 24$.

UNITED STATES. Florida: Hillsborough Co., *R18651* ($n = 24$).

Sect. *Miquelia*

Ludwigia ovalis Miq. ($n = 16$).

JAPAN. Kyushu: Prov. Satuma, *S. Hatusima 26593** ($n = 16$; *R18090*), *in 1966** (*R67-L1*).

Sect. *Nematopyxis*

Ludwigia prostrata Roxb. ($n = 8$).

INDIA. Dehra Dun, *P.C. Pant 38535**; Lachmansidh, Dehra Dun, *M.A. Rau** (BSI); Bihar, Champaran, Gobardhana, *Shetty 342* ($n = 8$; Shetty & Subramanyam, 1971).

Sect. *Nipponia*

Ludwigia epilobioides Maxim. subsp. *epilobioides* ($n = 24$).

CHINA. Taipeh, *J.M. Chao 1100** ($n = 24$; *R18126*). JAPAN. Honshu: Chiba Pref., *R18093** ($n = 24$); Kyoto, *H. Hara in 1961** ($n = 24$; *R18082*). Kyushu: Kagoshima, *S. Hatusima** ($n = 24$; *R18086*).

Ludwigia epilobioides subsp. *greatrexii* (H. Lév.) Raven ($n = 24$).

JAPAN. Honshu: Chiba Pref., *H. Hisauchi in 1961** ($n = 24$). Kyushu: Ossumi Pref., *S. Sako in 1961** (*R18083*).

Sect. *Oligospermum*

Ludwigia adscendens (L.) Hara subsp. *adscendens* ($n = 16$).

CHINA. Hong Kong* (no voucher, living plants sent by C. DeVol). INDIA. Without definite locality (M. Jash in Sharma & Sharma, 1966, as *Jussiaea repens*); West Bengal (2 localities; N. Datta *in litt.*). THAILAND. SE of Chiengmai, *Sørensen et al. 5018** (C).

Ludwigia adscendens subsp. *diffusa* (Forsk.) Raven [*L. stolonifera* (Guill. & Perr.) Raven] ($n = 16$).

GHANA. Nungua Dam, *Morton A4139** ($n = 16$; *R16670*); Accra Plains, *Morton A4139**. IRAQ. Amara Marshes, *Al-Rawi** (*R19656*). KENYA. Leita Dist., *Hocombe 1506** ($n = 16$; *R16771*). RHODESIA. Beitbudge Dist., *Drummond 6119** (K).

Ludwigia helminthorrhiza (Mart.) Hara ($n = 8$).

PANAMA. Gamboa, Canal Zone, *Dressler** (*R19653*).

Ludwigia hookeri (Mich.) Hara ($n = 8$).

BRAZIL. Florianópolis, Santa Catarina, *Sehnem 7** ($n = 8$).

Ludwigia peploides (H.B.K.) Raven subsp. *glabrescens* (O. Kuntze) Raven. Populations with $n = 8$.

TABLE 2. Continued.

FRANCE. Vias, Hérault, *L.Berner** (*R20133*). MEXICO. Chiapas: San Cristóbal las Casas, *Breedlove 7163**. Chihuahua: 14 mi W of Matachic, *Wiens 3462* ($n = 8$). UNITED STATES. Arkansas: Clark Co., *Demaree 48954** (*R19655*). Texas: Fort Bend Co., *R19404* ($n = 8$); Llano Co., *R19323* ($n = 8$); Presidio Co., *Gregory 224* ($n = 8$; Gregory & Klein, 1960).

Ludwigia peploides subsp. *glabrescens*. Populations with $n = 16$.

UNITED STATES. Mississippi: Jones Co., *R18573* ($n = 16$).

Ludwigia peploides subsp. *montevidensis* (Spreng.) Raven ($n = 8$).

AUSTRALIA. South Australia, *R18094**. CHILE. Nr. Farellones Ski Resort above Santiago, *Wiens** (*R67-L10*). UNITED STATES. California: Stanislaus Co., *R16610* ($n = 8$; Raven, 1963b).

Ludwigia peploides subsp. *peploides* ($n = 8$).

UNITED STATES. California: Rancho Santa Ana, Los Angeles Co. ($n = 8$; no voucher; Gregory & Klein, 1960); San Bernardino Co., *R in 1961** (RSA).

Ludwigia peploides subsp. *stipulacea* (Ohwi) Raven ($n = 8$).

JAPAN. Without definite locality (Sinotô, 1928). Honshu: Miura City, Kanagawa Pref., *S.Ohtani s.n.*

Ludwigia uruguayensis (Camb.) Hara. Populations with $n = 24$.

BRAZIL. Rio Grande do Sul, *Sehnem** (*RG62090*). UNITED STATES. Florida: Bradford Co., *R18693* ($n = 24$, multivalents common). Texas: Chambers Co., *R19423* ($n = 24$, multivalents common).

Ludwigia uruguayensis. Population with $n = 48$.

UNITED STATES. North Carolina: New Hanover Co., *Gregory 531* ($n = 48$, multivalents common).

Ludwigia uruguayensis. Populations with $n = 40$.

COSTA RICA. Just above Cartago on road to Irazú, *R22038* ($n = 40$). FRANCE. Unvouchered material from southern France, sent as living plants*. UNITED STATES. California: Los Angeles Co., Botanical Garden, University of California (no voucher; determined by M. Kurabayashi); Tiburon, Marin Co., *R16563* ($n = 40$; multivalents common); Stanford, Santa Clara Co., *R16590* ($n = 40$; multivalents common).

Sect. *Prieurea*

Ludwigia senegalensis (DC.) Troch. (*L. pulvinaris* Gilg) ($n = 8$).

SIERRA LEONE. Road from Morea Junction to Fintonia Natl. Park, *Morton SL586**. ZAMBIA. Kalabo, *Fanshawe F8060** (*R18725*).

Sect. *Seminuda*

Ludwigia affinis (DC.) Hara. Populations with $n = 32$.

BRAZIL. Terr. Amapá, Rio Araguari, *Pires et al. 51342** (NY). PERU. Nr. Iquitos, Dept. Loreto, *Dressler in 1964** (*R20675*).

Ludwigia affinis. Populations with $n = 40$.

SIERRA LEONE. *Morton SL848**. VENEZUELA. Caucagua, *Medina in 1964**.

Ludwigia africana (Brenan) Hara ($n = 24$).

ZAÏRE. Djombi-Djungu, *Déville 512** (BR; *R16772, R18095*).

Ludwigia leptocarpa (Nutt.) Hara. Populations with $n = 16$.

ECUADOR. Galápagos Islands, *Wiggins 18790* (DS). PANAMA. Barro Colorado I., *R.King** (*RG63028*). UNITED STATES. Alabama: Baldwin Co., *R18587* ($n = 16$). Arkansas: *Demaree 51267** (DS). Florida: Clay Co., *R18688* ($n = 16$); Taylor Co., *R18621* ($n = 16$); Walton Co., *Godfrey 57651** ($n = 16$; RSA; Gregory & Klein, 1960). Georgia: Pierce Co., *R18085** ($n = 16$), *Ahles in 1962**. Illinois: Massac Co., *Evers 82276** (*RG65-79*). Louisiana: St. Tammany Parish, *R18578* ($n = 16$). Mississippi: Lamar Co., *R18575* ($n = 16$).

Ludwigia leptocarpa. Populations with $n = 24$.

GHANA. Brinsu, *Hall 2864* (*R65-186*); nr. Weija. *Morton** ($n = 24$; DS; *R16668*).

[a] An asterisk indicates progeny grown in the experimental garden from the collection indicated.

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TAXONOMY AND DISTRIBUTION OF *CIRCAEA* (ONAGRACEAE) IN THE USSR[1]

A. K. Skvortsov[2]

Abstract

In the USSR, five species of *Circaea* are recognized: *C. alpina* L., *C. caulescens* (Kom.) Hara, *C. lutetiana* L., *C. cordata* Royle, and *C. mollis* Sieb. & Zucc. Also, the sterile hybrid *C.* × *intermedia* Ehrh. is known from several regions. Distribution areas of all these taxa are presented on maps based on herbarium materials studied by the author. Among these materials, no specimen of *C. erubescens* Franch. & Savat. has been detected, though this species had been reported from southern Sakhalin previously. *Circaea caucasica* A. Skvortsov, described by the author earlier, is now regarded to be a disjunct fraction of *C. caulescens*.

The genus *Circaea* has few species, and they are sharply delimited taxonomically and very distinct and uniform morphologically and ecologically. All *Circaea* species are tender, broad-leaved, shade- and moisture-loving herbs. The overall area of the genus closely coincides with the area of temperate mesophilic (broad-leaved, mixed, and dark-coniferous) forests of the northern hemisphere. Hence, from the study of taxonomic interrelations within the genus *Circaea,* one could expect to get interesting suggestions regarding the history of mesophilic temperate forest in general.

I have been interested in *Circaea* for many years, and have previously published a few short notes on the subject (Skvortsov 1970, 1971, 1977). The present paper provides a general taxonomic and geographical review of this genus within the USSR.

I have studied *Circaea* both in the field and in herbaria. Field observations have been made chiefly in the following regions of the USSR: central part of the European territory (provinces of Moscow, Kaluga, Smolensk); Ukrainian Carpathians; Crimea; central part of the Great Caucasus; Altai Mountains; southern part of the Soviet Far East (Primorski Province). Outside the USSR, I have had the opportunity to observe and to collect *Circaea* species in Sweden, in the Indian Himalayas, and in the southern Appalachians.

Herbarium materials of the following institutions have been studied in full: Komarov Botanical Institute in Leningrad (LE); Botanical Institutes in Kiev (KW), Minsk (MSK), Erevan (ERE), and Wilnius; Biological Institutes in Riga (LATV), Syktyvkar (SYKO), and Vladivostok (VLA); Institute of Zoology and Botany in Tartu (TAA), Institute of Ecology in Sverdlovsk (SVER), Siberian Institute of Plant Physiology and Biochemistry in Irkutsk (IRK), Main Botanic Garden in Moscow (MHA), Central Siberian Botanic Garden in Novosibirsk (NS); Universities of Moscow (MW), Leningrad (LECB), Tartu (TU), Riga (RIG), Wilnius (WI), and Vladivostok. In part, materials also have been studied from the Universities of Uppsala (UPS) and Lund (LD).

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The distribution maps presented in this paper are based on herbarium specimens I have examined.

1. *Circaea alpina* L.

Among the members of the genus, this species has the largest area of distribution. The distribution area of *Circaea alpina* has been depicted earlier by Tolmachev (1954: 71), Hultén (1971: map 86), and Jäger (1969 : 404). As compared with these earlier maps, my map (Fig. 1) provides some necessary additions and corrections.

In the most generalized manner, the distribution of *Circaea alpina* may be termed circumpolar holarctic-boreal. A closer examination reveals some interesting details. In the middle of the Eurasian continent the zone occupied by *C. alpina* is the narrowest: less than 10° of latitude. In contrast, towards the western and eastern flanks of Eurasia, along with the decrease of the continentality and increase of the "maritimity" of the climate, the latitudinal span of the *C. alpina* area reaches nearly 30° (in the West from 40–41° N in Italy, northeastern Turkey, and Soviet Armenia to 70°N in Norway; in the East from 32–33°N in Kyushyu and Quelpaert Islands to 59°N in Koraginski Island. A similar pattern may be observed in the Western Hemisphere also.

In Transbaicalia there seems to exist a considerable (250–300 km wide) gap in the distribution of *Circaea alpina*. The region in question is by no means an unexplored one; thus, even if *C. alpina* will be some day found here, there will be only isolated localities. Though the chorology of the forest flora in Transbaicalia is yet far from fully worked up, still a few other Eurasian mesophytic forest species can be mentioned which have quite similar gaps in their areas, viz., *Salix caprea* (map: Skvortsov, 1968: figs. 9, 40), *Pyrola secunda* (maps: Skvortsov, 1960, 1968: fig. 9), *Oxalis acetosella* (map: Tolmachev, 1954: 64).

Southern Yakutia, too, is not underexplored, especially as regards the valleys of the larger rivers. The scarcity of *Circaea alpina* here is to be explained by the dryness of the climate and the resulting very restricted distribution of the dark coniferous taiga.[3]

In the USSR *Circaea alpina* usually inhabits shady and humid, but not boggy or marshy, places in coniferous or mixed forests. Often it can be seen on decaying stumps, rocky outcrops, or stony debris (especially calcareous) amidst a forest, or in shady ravines. More rarely it can be found in broad-leaved deciduous forests or in birch groves. In the northern parts of its area and in Siberia it prefers the dark taiga; nearer to the southern edge of its area, especially in the European part, *C. alpina* often grows in wet (sometimes even swampy) alder groves ("Erlenbrüche" of the German authors). It always grows in patches, never forming a continuous layer in a given forest plot.

Only extremely rarely does *Circaea alpina* reach the alpine region. In the Caucasus it has been found in subalpine birch elfinwood groves or among rocks

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[3] In Russian literature, the term dark taiga denotes coniferous forest composed of more hydrophilic and densely crowned trees: spruce, fir, and Siberian cedar-pine (*Pinus sibirica*). Light taiga is formed by more loosely crowned and relatively xerophilic larches and *Pinus silvestris*. The distinction between these two types is very important ecologically and phytogeographically.

FIGURE 1. Distribution of *Circaea alpina* in the Soviet Union.

up to 2,300–2,400 m. In the Urals, or Siberian, or Far Eastern mountains no alpine or subalpine localities have been recorded. Excepting the northeastern extremity of its Asian range, nowhere else in the USSR does it approach northern forest limits.

In the central and southern regions of the European part of the USSR the distribution of *Circaea alpina* seems to have been continuously shrinking during the nineteenth and twentieth centuries, and it is quite possible that the distribution presented in Fig. 1 in part reflects not entirely the present but perhaps even now some past situations. On the contrary, in the Far East *C. alpina* seems to fit quite well into the present ecological situation. So, it remains quite common in the southern part of the Primorski Province, including the nearest outskirts of Vladivostok, despite increasing human pressure.

In the course of the intensive floristic investigation of the Soviet Far East in the post-war period, *Circaea alpina* has been discovered in nearly all of the Kurile Islands, from Zeleny (Shihotsu) and Kunashir to Shumshu. Quite remarkable is the recent discovery of *C. alpina* on the completely treeless Koraginski Island (*Voroshilov et al.* in 1969, MHA); it grows there in low shrubby thickets amid herbaceous tundra. It is rather widespread in the Island of Sakhalin, as well as in Japan. Thus the opinion expressed by Hara (1934), Ohwi (1965), and, more reservedly, by Voroshilov (1966), that the Far Eastern distribution of *C. alpina* is predominantly continental, seems to be unjustified. On the contrary, *C. alpina* is more widespread in the maritime climate of the islands.

Especially interesting is the occurrence of *Circaea alpina* on Kyushyu. Two specimens I have seen from this island—Nagasaki–Simbaru (= Shimabara), *Maximowicz* in 1863, and Mount Hiko-san, *Makino* in 1906 (both LE)—undoubtedly belong to *C. alpina*. Equally interesting is the presence of this species on Quelpaert Island (Cheju-do) where it had been collected on Mount Hallaisan at altitudes from 1,300 to 1,700 m (*Taquet 832, 4258,* LE). This makes one suspect that *C. alpina* might be present even in Taiwan.

The morphological characters of *Circaea alpina* are rather uniform throughout its whole holarctic area. In Eurasian materials, I have been able to discover only one character having significant geographical variability: the quantity of glandular pubescence in the inflorescence. In Europe, Caucasus, and Siberia this pubescence is well developed, but in the Far East it is usually scarce or even absent.

The plants of Southwestern China, Tibet, and drier inner chains of the Himalayas, formerly referred to *Circaea alpina,* in my opinion should be regarded as a separate species, *C. micrantha* A. Skvortsov (1977). These plants have very small, entire or only slightly emarginate petals (resembling those of *C. erubescens* Franch. & Savat.). Between the areas of *C. alpina* and *C. micrantha,* there is a disjunction of about 1,000 km or even wider.

2. *Circaea caulescens* (Kom.) Hara

In 1905, V. L. Komarov, based on a plant collected by himself in northern Korea and two specimens collected by D. I. Litvinov in northeastern China described *Circaea alpina* var. *caulescens* Kom. As the chief distinction of the variety from the typical *C. alpina,* he emphasized its taller and more erect stem. In 1934, Hara raised the variety to the rank of species under the name *C. cau-*

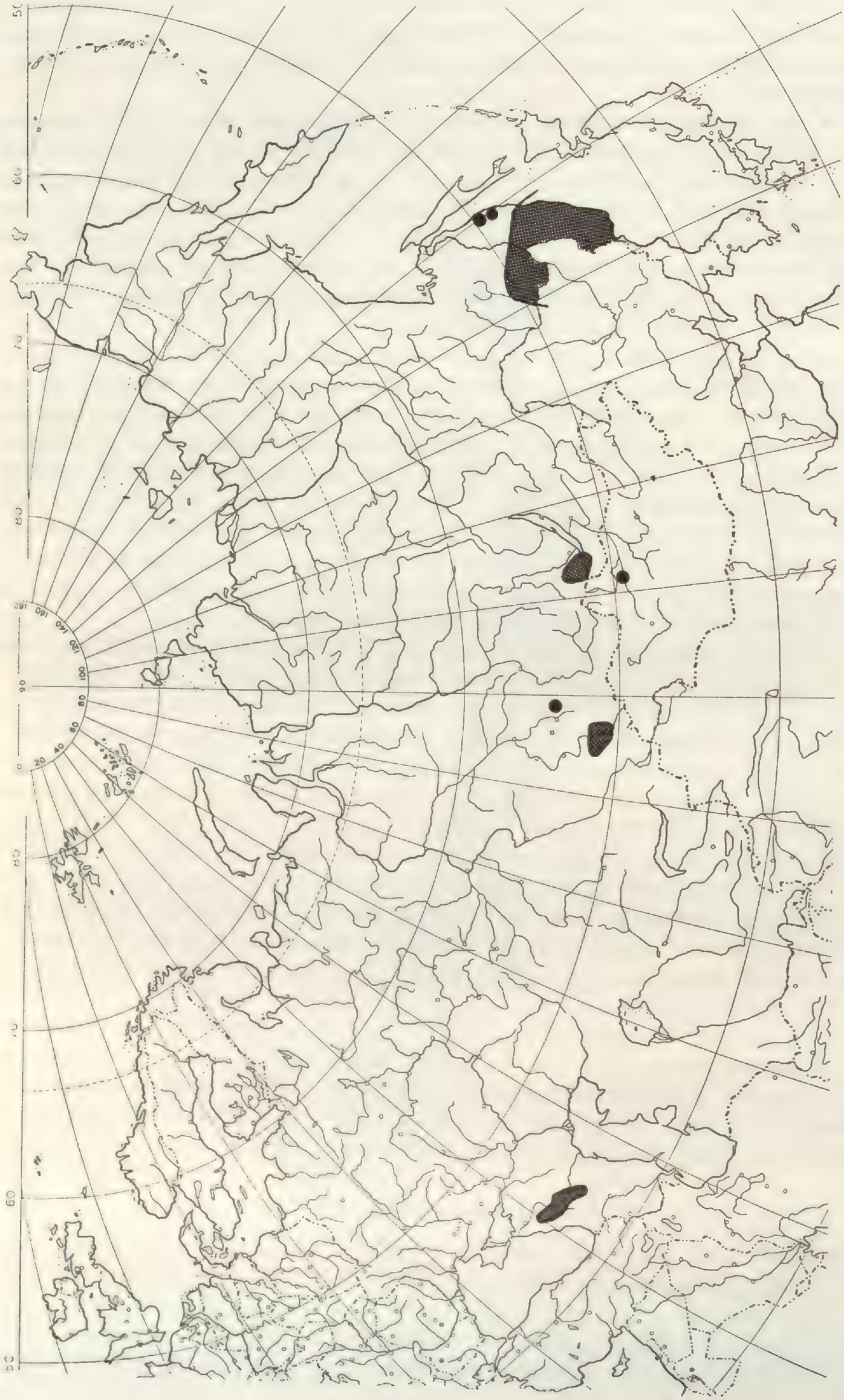

FIGURE 2. Distribution of *Circaea caulescens* in the Soviet Union.

lescens (Kom.) Nakai ex Hara. Neither Komarov nor Nakai nor Hara, however, properly clarified the morphological differences between *C. alpina* and *C. caulescens*. Consequently, Hara quite erroneously believed that these species are vicarious and that in Japan (and even in the entire Far East) only the latter species is widespread. This opinion was also expressed by Ohwi (1965: 655). Actually, as has been pointed out above, *C. alpina* is very widespread in the Far East. In contrast, *C. caulescens* has a very restricted area on the continent, and is absent from the Soviet Far Eastern islands. It also seems to be quite rare in Japan. Among herbarium materials from Japan that I have had access to, I detected specimens of *C. alpina* from ten localities, but not a single specimen of *C. caulescens*.

Circaea caulescens has a nonglandular pubescence of reflexed sicklelike hairs on the stems below the inflorescence. *Circaea alpina* never has such a pubescence on the stems. The flowers of *C. caulescens* are larger, usually pink or purplish, and open in a lateral position, whereas the small and usually purely white flowers of *C. alpina* open while directed upwards. The leaves of *C. caulescens* are darker and nontransparent, while the leaves of *C. alpina* usually are lighter colored and translucent when dried.

In 1970 I described what I believed to be a new species, *Circaea caucasica*. Since then, after having studied additional materials, especially from Siberia, I have concluded that *C. caucasica* should be included in *C. caulescens*. Whether it might be regarded a subspecies, remains to be seen.

The total area of *Circaea caulescens* consists of four widely disjunct fragments (Fig. 2): (1) Far East; (2) Baical and northern Mongolia; (3) Altai; (4) central and western part of the Great Caucasus. This is an extremely interesting and very rare type of distribution, that is probably most closely matched by the distribution of *Osmorhiza aristata* (Thunb.) Makino & Yabe (Umbelliferae). The latter species also has its main area of distribution in the Far East, with small fragments in the Altai and in the western part of the Great Caucasus.

Ecologically *Circaea caulescens* resembles *C. alpina* closely.

Quite often the two species grow intermingled; I have seen this many times in the Primorski Province, in the Altai, and in the Caucasus. But no intermediates have been observed in such cases, nor among herbarium specimens. It seems that *Circaea caulescens* generally prefers drier and warmer situations than does *C. alpina*.

The Himalayan *Circaea imaicola* (Aschers. & Magnus) Hand.-Mazz. and the western North American *C. pacifica* Aschers. et Magnus are closely related to *C. caulescens*. All three should be regarded as descendants of a common ancestral stock, evidently a Tertiary warm-temperate one, whereas *C. alpina* and *C. micrantha* A. Skvortsov are descendants of another stock, probably a Pleistocene cold-temperate one. The third, and seemingly the most ancient relic stock of the *Uniloculares* group, is the Himalayan and South Chinese *C. repens* Wall. The origin of the *Uniloculares* (i.e., its divergence from the *Biloculares*) group must have taken place somewhere in southeastern Asia about the beginning of the Neogene.

3. *CIRCAEA LUTETIANA* L.

Like *Circaea alpina,* this species has a holarctic distribution but—in contrast to *C. alpina*—with many wide disjunctions. As has already been shown by Jäger (1969), the whole group *Biloculares,* to which *C. lutetiana* belongs, is very distinctly associated with the main regions of temperate deciduous broad-leaved and mixed (i.e., coniferous + broad-leaved) forests. The total range of the group resembles the area of the genus *Tilia* (Jäger 1969: figs. 4–5).

In the USSR, *Circaea lutetiana* has four main regions of distribution (Fig. 3): (1) Mixed and broad-leaved forests of the Russian Plain up to the foothills of the Urals; (2) mixed and broad-leaved forests of Crimea and Caucasus; (3) rich dark taiga or deciduous forest of the Altai-Sayan region of Siberia; (4) mixed and broad-leaved forests of the southern part of the Soviet Far East.

Besides these main fragments there are a number of disjunct isolated localities, the most interesting being those in the Saur Range (south of Lake Zaisan), in the Dzhungarian Range, and near Bayan-Aul in the hilly plateau ("Melkosopochnik") of the northern Kazakhstan.

Among old nineteenth-century collections preserved at LE, there are three intriguing specimens of *Circaea lutetiana*:

1. "Turcomania, *Karelin*." At present, the species is not known in Turcomania (Turkmenia), though the tip of its Iranian area approaches the USSR borders very closely. Perhaps Karelin collected the plant on what is now Iranian territory—or *C. lutetiana* may indeed have been growing in Turkmenia and subsequently died out.

2. "In deserto Kalmykorum inter Volgam et Ural, Sergatscheff (Reliq. *Fischer*)." Beyond the Volga towards the Ural River in the midst of dry treeless steppe, there is indeed a place where many forest plants find shelter—the so-called Saltovski Forest on sandy terraces of the Eruslan River (northeast of Kamyschin, at the border between the provinces of Saratov and Volgograd). Has the plant indeed been collected here? If so, this would be extremely interesting, and still more so because in its morphology the plant resembles mid-European or Caucasian specimens rather than eastern-European ones.

3. "In nemoribus humidis haud procul a Syuzma, Archangel, *Bohuslaw* in 1844." Syuzma is situated west of Arkhangelsk at the White Sea coast. The record seems to be quite improbable because the locality is so far north. But one should keep in mind that even farther north, at the so-called Zimni Bereg (Winter Coast) of the White Sea, there is a disjunct fragment of the area of *Epilobium montanum* (Skvortsov, 1976), and a number of other temperate forest species (*Alnus glutinosa, Anemone ranunculoides, Corydalis solida, Viola mirabilis,* etc.) reach the southern coasts of the White Sea.

Circaea lutetiana requires rich, deep, and humid soil. In the European part of the USSR its usual habitat is in the bottoms of forested ravines, especially if they contain small rivulets; in Siberia the most usual habitat is alluvial forests.

If typical mid-European plants are compared with Far-Eastern ones, it can be easily seen that the latter are less pubescent, and have more elongated leaves and less attenuate bases of nutlets; the nutlets are conspicuously ribbed to grooved. Based on these differences, Maximowicz (1859:106) established for the Far-Eastern plants the "forma *quadrisulcata*"; Franchet & Savatier (1875:169) elevated

FIGURE 3. Distribution of *Circaea lutetiana* in the Soviet Union.

it to specific rank. Following them, twentieth-century Russian literature usually accepts the existence of two vicarious species: the European-Caucasian *Circaea lutetiana* L. s. str., and the Far-Eastern *C. quadrisulcata* (Maxim.) Franch. & Savat. Many foreign authors regard the latter as a variety or subspecies. The status of the Siberian populations remains obscure from any viewpoint; usually they are tacitly accepted as belonging to the European race.

I long ago had come to the conviction that *Circaea quadrisulcata* cannot be maintained as a species. But as to recognition of subspecies, the situation seemed to me doubtful. The pattern of morphological variability had to be carefully considered against the geographical background. Hence, in the course of preparation of the present paper the variability of *C. lutetiana* has received special attention.

A most surprising fact is that plants from the central region of the European part of the USSR look more like Far-Eastern than central-European ones. This fact had also been noticed by Dr. P. H. Raven, who insistently drew my attention to it.

Circaea lutetiana has two types of hairs on the stem: glandular and nonglandular. Glandular pubescence is chiefly developed in the inflorescence; in its variability I did not notice any regularity. Nonglandular pubescence usually is best developed just below the inflorescence and decreases upwards (into the inflorescence) and downwards (to the base of the stem). The denser the pubescence, the more it is spread upwards and downwards. Typically, the nonglandular hairs are sicklelike and recurved backwards.

From the Far East and up to the provinces of Moscow and Kaluga, in all plants rather uniformly, the nonglandular pubescence is sparse. But in the Baltic region, Belorussia, and the western half of the Ukraine, along with the sparsely pubescent plants of the Eastern type, plants with much more developed pubescence, the Western type, also begin to be seen. In cases where the pubescence is especially dense, the hairs change their form and position and become straight and patent so that the stem looks villous. Such plants have been described as var. *villosa* Beck, Fl. Nied.-Oesterr. 695. 1893. In the western regions of the USSR var. *villosa* has been collected many times: in Moldavia, in the Carpathians, near Lvov, in the Crimea, and even at Kanev (on the Dnepr River below Kiev). I also have seen villous specimens from Poland, Hungary, Yugoslavia, and Switzerland.

The central European type of the leaf blade (broadly rounded or cordate at the base) and of the fruit (pyriform, with attenuate base and grooves little pronounced) also can often be encountered in the westernmost regions of the USSR; in the Crimea, Moldavia, and the Carpathians these forms dominate. But the Western types of leaf base and fruit form are not necessarily equally pronounced in the same individuals; nor are they necessarily accompanied by the Western type of pubescence.

Plants with the Eastern type of leaf blade and pubescence seem to be not too rare yet in Poland (such are, for instance, specimens from the Gostynin district in central Poland distributed by *Woloszczak* as Fl. Polon. exs. N628, and from Ojców near Krakow collected by *Ganeshin* in 1905, LE). Specimens with fully developed fruits are not very numerous in herbaria. Still, I was able to trace a purely Eastern type of fruit (globose with very pronounced ridges and grooves) as far west as the Alps ("Lienz in Tirol," *Gander*, without date, LE).

In the Caucasus, plants of the Western type are prevalent, though a wide range of variability can be observed. The villous type of pubescence is rather frequent. In the few Iranian specimens I have seen nonglandular pubescence is quite sparse.

To sum up, any distinct demarcation line between the Eastern and Western morphological types of *C. lutetiana* cannot be drawn. Hence, there seems to be no good reason to recognize any intraspecific taxonomic entities. The situation can be more adequately portrayed in a descriptive manner in terms of character geography and frequencies.

4. *Circaea* × *intermedia* Ehrh.

This sterile hybrid between *Circaea alpina* and *C. lutetiana* is quite common in central and Atlantic Europe but rather rare in the USSR. This may be explained by the fact that in the USSR the two species are ecologically differentiated and only very rarely can be observed growing together or in close proximity to each other. Most of the known localities of *C. intermedia* in the USSR are concentrated in the West (Fig. 4). In all, I have seen 23 gatherings from the European part of the USSR (representing probably some 20 different localities); in the Caucasus there are seven known localities, and in the Far East only three. Evidently, the occurrence of *C. intermedia* is associated with more humid climates and is chiefly a European phenomenon.

I have observed *Circaea intermedia* in natural habitats in two localities that I discovered in the central region of the European part of the USSR. Both are situated in the valley of the Ugra River: one in the province of Smolensk (near the village Zhelanya), and another in the province of Kaluga (near the village Palatki). In both localities *C. intermedia* grows alone, without either of the parental species in its immediate neighborhood. In the first locality neither of the parents could be found closer than at least 1 km around the population of *C. intermedia*. In the second locality, *C. lutetiana* has been found at a distance of 400 to 500 m, but *C. alpina* was nowhere around.

Clonal populations of *Circaea intermedia* can persist for quite considerable periods and thus may have originated long ago. The above mentioned locality in the province of Smolensk was first seen by me in 1938 (Skvortsov, 1961)—the very first year I began plant collecting in the surroundings of my native village. In 1978 I revisited the place. Although the habitat had been much altered by wood cutting and cattle grazing, *C. intermedia* still persisted.

A similar persistence of *Circaea intermedia* in the absence of the parental species has been repeatedly recorded in western European literature (see especially Raven, 1963; Jungblut, 1967). The explanation of this phenomenon may be sought in climatic changes or in interference of man causing the decline of parental species, or in an interaction of both factors. But fairly certainly some kind of hybrid heterosis should also be taken into consideration.

5. *Circeae mollis* Sieb. & Zucc.

Regarding the presence of this species in the USSR flora, very divergent opinions have existed. The situation was clarified in my previous paper (Skvort-

FIGURE 4. Distributions of *Circaea* × *intermedia* (dots), *C. mollis* (asterisk) and *C. cordata* (shaded area) in the Soviet Union.

sov, 1977). The species has been collected in the USSR twice, both localities being situated near the southern edge of Lake Hanka (Fig. 4).

6. *Circaea cordata* Royle.

This species is rather common in the southernmost part of Primorski Province, including the islands in the Gulf of Peter the Great. Towards the north it quickly becomes rare; the northernmost locality is Mount Vandan about 60 km north of Khabarovsk. The species has not been found on Sakhalin Island, but occurs on the small Moneron Island near the southwestern edge of Sakhalin, and on Kunashir Island.

Compared with *Circaea lutetiana*, *C. cordata* prefers better drained and open habitats, often along forest edges. In spite of its quite extended distribution, the species seems to display no significant geographical variability. Specimens I collected in several localities in Kashmir cannot be discriminated from plants collected near Vladivostok.

7. *Circaea erubescens* Franch. & Savat.

According to Hara (1934: 592), this species was collected by Sugawara near Toyohara (now Yuzhnosakhalinsk). In the USSR herbaria (LE, MHA) there are two specimens collected near Yuzhnosakhalinsk which could have been suspected to belong to *Circaea erubescens*: (1) An unidentified Japanese collector, 30. Aug. 1931 (ex Herb. Saghalien Experim. Station); (2) *V. N. Voroshilov*, 7 Oct. 1953. Voroshilov (1966) evidently influenced by Hara's views, believed these specimens to be *C. erubescens*, and consequently included the species in his *Flora of the Soviet Far East*. But at the same time Voroshilov thought that *C. erubescens* might have originated as a hybrid between *C. alpina* and *C. quadrisulcata*. In my opinion, both specimens are *C.* × *intermedia* and differ distinctly from *C. erubescens*. Thus there is no evidence of the existence of *C. erubescens* in the USSR.

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A SECTIONAL REVISION OF *LUDWIGIA* SECT. *MYRTOCARPUS* S. LAT. (ONAGRACEAE)[1]

T. P. RAMAMOORTHY[2]

ABSTRACT

Ludwigia sect. *Myrtocarpus* (Onagraceae), hitherto taken in an inclusive sense, is here divided into seven sections, all confined to or centering in South America. Four of these sections—*Amazonia (L. densiflora)*, *Heterophylla (L. inclinata)*, *Humboldtia (L. sedoides)*, and *Tectiflora (L. latifolia)*—are monotypic and of uncertain relationship to one another and to the other portions of the genus, although it is possible that *Tectiflora* is related to one of the more generalized groups into which sect. *Myrtocarpus* is here divided. The remaining three sections, *Myrtocarpus* s. str., *Michelia*, and *Pterocaulon*, do seem to be interrelated to one another and to the ditypic African sect. *Africana*, but their similarity is based mainly upon their retention of generalized features. The least specialized section of the genus is sect. *Myrtocarpus* s. str., but the only section of this part of the genus in which genetic self-incompatibility is retained is sect. *Michelia*.

Ludwigia (Onagraceae), the only genus of the very distinctive tribe Jussiaeeae, represents an evolutionary line separate from all other genera of the family (Raven, 1963, 1979; Eyde, 1977; Raven & Tai, 1979). It has some 80 species of pantropical distribution with some distinctive elements in temperate Eurasia and especially North America. Within this genus, the primarily South American sect. *Myrtocarpus* (Munz, 1942; Raven, 1963) has been the largest (with 23 species) and most heterogeneous.

In the light of my recent biosystematic investigations, it now appears that *Ludwigia* sect. *Myrtocarpus*, in the traditional sense, is a partly artificial group, some elements of which are held together only by their common possession of a series of plesiomorphic characteristics ("a preponderance of ancestral features," Eyde, 1978). These are primarily the unspecialized capsules with their pluriseriate ovules and narrow raphe. Data from artificial hybridization and a more detailed morphological study than was possible earlier has resulted in the detection of seven distinct groups within what has been regarded as sect. *Myrtocarpus*, each comparable with the 16 other sections of *Ludwigia* (Raven, 1963), as well as with the kind of relatively close-knit, presumably monophyletic sections that have been utilized in the classification of other genera of the family (e.g., Lewis & Lewis, 1955; Raven, 1969, 1976). Although the sections *Myrtocarpus* s. str., *Michelia*, and *Pterocaulon* as recognized in this paper are probably directly related to one another and to the ditypic African sect. *Africana* (Raven, 1963), they are sharply distinct morphologically, and it has not been possible to obtain artificial hybrids between them. The sections which I recognize for the species included by Raven (1963) in sect. *Myrtocarpus*, and their principal included species, are as follows:

Ludwigia sect. **Myrtocarpus** (Munz) Hara, J. Jap. Bot. 28: 291. 1953. Based on *Jussiaea* sect. *Myrtocarpus* Munz, Darwiniana 4: 184. 1942.

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Type species: *L. peruviana* (L.) Hara.

Perennials. Sepals 4–5(–6). Petals 4–5(–6). Stamens 8–10(–12). Capsule thin walled, 4-angled to terete, irregularly dehiscent. Seeds oblong, sometimes curved. Self-compatible.

Included species: *Ludwigia bullata* (Hassler) Hara, *L. burchellii* (Mich.) Hara, *L. caparosa* (Camb.) Hara, *L. elegans* (Camb.) Hara, *L. foliobracteolata* (Munz) Hara, *L. laruotteana* (Camb.) Hara, *L. peruviana* (L.) Hara, *L. sericea* (Camb.) Hara, *L. tomentosa* (Camb.) Hara.

Ludwigia sect. **Michelia** T. P. Rammmoorthy, sect. nov.

Type species: *L. nervosa* (Poir.) Hara.

Herbae perennes. Sepala 4. Petala 4. Stamina 8. Capsula pariebus relative tenuibus, plus minusve 4-angulata, teres vel suburceolata, irregulariter dehiscens. Semina oblonga curvata.

Included species: *Ludwigia anastomosans* (DC.) Hara, *L. brachyphylla* (Mich.) Hara, *L. myrtifolia* (Camb.) Hara, *L. nervosa* (Poir.) Hara, *L. rigida* (Miq.) Sandwith.

This section consists mainly of large woody plants, essentially shrubs, in which genetic self-incompatibility predominates. The name commemorates M. Micheli (1844–1902), who prepared the important treatment of "*Jussiaea*" for Martius's *Flora Brasiliensis* (1875).

Ludwigia sect. **Pterocaulon** T. P. Ramamoorthy, sect. nov.

Type species: *L. erecta* (L.) Hara.

Herbae annuae. Caules manifeste 4-angulati melius alati. Sepala 4. Petala 4. Stamina 8. Capsula relative pariebus relative tenuibus, conspicue 4-angulata anguste alata, irregulatiter dehiscens. Semina oblonga exigue curvata.

Included species: *Ludwigia decurrens* Walt., *L. erecta* (L.) Hara, *L. longifolia* (DC.) Hara, *L. mexiae* (Munz) Hara.

This section consists of subglabrous, weedy, self-pollinating, mostly annual species that are clearly distinct from but likely derived from plants similar to those included in sect. *Michelia*. The name of the section refers to its 4-angled or 4-winged stems and capsules.

Ludwigia sect. **Tectiflora** T. P. Ramamoorthy, sect. nov.

Type species: *L. latifolia* (Benth.) Hara.

Herbae vel frutices erectae. Sepala 4. Petala 4. Stamina 8. Contextus sporogenus antherae in loculis subdivisus; antherae pilis longis vestitae. Capsula pariebus crassis subtarde dehiscens subglobosa. Semina oblongo-obovoidea.

Only species: *Ludwigia latifolia* (Benth.) Hara.

This species shares with the completely unrelated *L. linearis* Walt. the distinction of being the only member of the genus *Ludwigia* in which the sporogenous tissue of the anthers is divided into packets longitudinally by sterile tissue, as in *Hauya* and four genera of the tribe Onagreae, *Clarkia*, *Heterogaura*, *Gaura*, and *Calylophus*. It is apparently the only member of the genus, and perhaps also

of the family, with pubescent anthers. The sectional name refers to the fact that the flowers are more or less hidden at the bases of the subtending leaves.

Ludwigia sect. **Heterophylla** T. P. Ramamoorthy, sect. nov.

Type species: *L. inclinata* (L.f.) Raven.

Herbae aquaticae caulibus natantibus ad nodos radicantibus. Folia basalia (saepe submersa) verticillata 4 ad eadam nodam; folia superiora alternantia latioria. Sepala 4. Petala 4. Stamina 4 vel 8. Capsula pariebus relative tenuibus, irregulariter dehiscens, aliquantum 4-angulata. Semina oblonga recta.

Only species: *Ludwigia inclinata* (L.f.) Raven.

This is a very distinctive species of uncertain affinities. In no other species of the genus are the lower leaves whorled. *Ludwigia verticillata* Munz, originally assigned to sect. *Dantia,* refers to a form of this species in which the epipetalous anthers have been lost; P. H. Raven (pers. comm.) has studied populations in marshy places on the Isthmus of Tehuantepec in Oaxaca, Mexico, in which plants with 4 stamens occur intermingled with others with 8 stamens, and are indistinguishable otherwise. As in many aquatic species, the morphology is highly variable, and the name *Ludwigia potamogeton* (Buchell ex Mich.) Hara, here relegated to synonymy, has been used to refer to plants with somewhat narrower leaves and less inflated stems. This species is primarily autogamous and is the only one in the genus in which two types of leaf arrangement occur, whence the sectional name.

Ludwigia sect. **Humboldtia** T. P. Ramamoorthy, sect. nov.

Type species: *L. sedoides* (Humb. & Bonpl.) Hara.

Herbae aquaticae caulibus natantibus ad nodos radicantibus. Folia integra rosula terminalia conferta. Sepala 4. Petala 4. Stamina 8. Capsula pariebus tenuibus 4-angulata irregulariter dehiscens. Semina obovoidea curvata.

Only species: *Ludwigia sedoides* (Humb. & Bonpl.) Hara.

This is a most attractive species, with its beautiful symmetrical floating rosettes and large yellow flowers. It is probably mainly self-pollinating, since the anthers surround the stigma, but I have no direct information on this point. Its affinities within *Ludwigia* are obscure. The section is dedicated to the memory of that intrepid explorer of Latin America, Alexander von Humboldt (1769–1859), who first discovered it in Colombia and later described it.

Ludwigia sect. **Amazonia** T. P. Ramamoorthy, sect. nov.

Type species: *L. densiflora* (Mich.) Hara.

Herbae annuae erectae. Flores spica brevo dispositi. Sepala 4–6. Petala 4–6. Stamina 8–12. Capsula pariebus crassis lineatis tarde dehiscens teres ad extremos angustata. Semina oblonga recta.

Only species: *Ludwigia densiflora* (Mich.) Hara.

This remarkable highly self-pollinating species is the only member of the genus that is confined to the Amazon Basin, whence the sectional name. Its capsular morphology is without parallel in the genus, the strong ribs and very tardy de-

hiscence being unique. The variability in flower part number may suggest a relatively great antiquity for the evolutionary line leading to this species, despite the evident specializations in the habit and the morphology of the capsule.

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NOTES

A NEW COMBINATION IN *EPILOBIUM* (ONAGRACEAE)

In his sectional delimitation of the genus *Epilobium*, Raven (1976) reduced the diploid ($n = 15$) *Zauschneria septentrionalis* Keck to a subspecies of the polymorphic diploid and tetraploid ($n = 30$) *E. canum* (Greene) Raven. We agree with most aspects of his interpretation, but have concluded as a result of detailed field and herbarium studies that *Zauschneria septentrionalis* should be treated as a distinct species. It is entirely allopatric with *E. canum* s. lat., although the two entities occur within about 200 m of one another along the Trinity River and the South Fork of the Eel River. The more local diploid is characterized by a distribution on rock ledges in the valleys of the Eel, Mattole, and Trinity rivers of Humboldt, Mendocino, and Trinity counties, California, at elevations from 20 to 125 m. It can readily be distinguished from all phases of *E. canum* by a combination of its distinctive short but suffruticose habit, subentire leaf margins, and white-canescent pubescence on the lower leaves. We therefore propose the following new combination, in anticipation of a more complete sectional revision, and in order to make the name available.

Epilobium septentrionale (Keck) Bowman & Hoch, comb. nov. Based on *Zauschneria septentrionalis* Keck, Publ. Carnegie Inst. Wash. 520: 219. 1940.

Epilobium canum (Greene) Raven subsp. *septentrionale* (Keck) Raven, Ann. Missouri Bot. Gard. 63: 335. 1976.

We agree with Raven (1976) in treating the remainder of *Epilobium* sect. *Zauschneria* as a single species, *Epilobium canum*. Our treatment of the diploid *E. canum* subsp. *garrettii* (A. Nels.) Raven, of the Great Basin, and the tetraploid *E. canum* subsp. *latifolium* (Hook.) Raven, mostly of the Sierra Nevada and northern Coast Ranges, follows that of Raven (1976) and others exactly. Our studies have led us to the conclusion, however, that *E. canum* subsp. *canum* should be treated in a much more inclusive sense. Here we place both the diploid, previously treated as *E. canum* subsp. *canum*, as well as the morphologically indistinguishable tetraploid, treated by Clausen et al. (1940) as *Zauschneria californica* subsp. *angustifolia* Keck. In addition, because of its complex intergrading pattern of variation, we have also included within this subspecies the often broad-leaved plants, partly with a more northern distribution, that have been treated as *Zauschneria californica* subsp. *typica* Keck (Clausen et al., 1940), *Zauschneria californica* subsp. *mexicana* (Presl) Raven (Raven, 1962), or *Epilobium canum* subsp. *mexicanum* (Presl) Raven (Raven, 1976). Great variability exists among these plants in stature; size, shape, and distribution of the leaves; vestiture; and other characters; but not even a combination of them consistently delimits clear taxonomic patterns. Following detailed study of the populations involved in the herbarium, it seems preferable to retain all within the limits of a single variable subspecies.

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CHROMOSOME NUMBER IN TWO PRIMITIVE DICOTS, *XYMALOS MONOSPORA* (MONIMIACEAE) AND *PIPTOCALYX MOOREI* (TRIMENIACEAE)

Xymalos monospora (Harvey) Baill. $2n = 40–42$. Zimbabwe-Rhodesia, Bunga Forest, Umtali distr., *Müller s.n.* (13 Aug. 1978) (SRGH).

Chromosomes of *Xymalos* are small in size, ranging from 1.5–2.5 μm and comparable in appearance to those of other Monimiaceae studied by Goldblatt (1974). Small size and high number made an accurate count for *Xymalos* difficult, especially as the material available was very limited.

Piptocalyx moorei Oliver ex. Benth. $2n = 16$. Australia, New South Wales, North Coast, *Floyd 1104* (NSW).

The chromosomes of *Piptocalyx* are substantially larger than those of *Xymalos* and range from 3–4.5 μm in size. Details of chromosome morphology are clearly visible and are illustrated in Fig. 1.

Xymalos is a monotypic genus of eastern south-tropical Africa, usually assigned to Monimiaceae s.l. The only other African genus is the tropical West African *Glossocalyx*, one of three genera of Monimiaceae-Siparunoideae (sometimes segregated as Siparunaceae); however, Monimiaceae-Monimioideae are well represented on the offshore African islands of Madagascar and the Mascarenes. An alternative systematic position for *Xymalos* was proposed by Hutchinson (1964) who placed the genus in the otherwise Pacific family Trimeniaceae. This treatment is not generally accepted (Schodde, 1970; Thorne, 1974) but was followed by Dyer (1975) in his revised generic flora of southern Africa.

There are strong cytological differences between Monimiaceae and Trimeniaceae, the former having base numbers at a palaeohexaploid level, $x = 22–19$. Base numbers for Monimiaceae s.s. (excluding Siparunaceae, $x = 22$, and Atherospermataceae, $x = 22$) are mostly $x = 19$ with counts also for $n = 22$ and $n = 18$ in two genera (Ehrendorfer et al., 1968; Goldblatt, 1974), while Trimeniaceae

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FIGURE 1. Chromosome morphology of *Piptocalyx moorei* at mitotic metaphase.

are evidently palaeodiploid, the only previous count being a report of $n = 8$ in *Trimenia papuana* (Goldblatt, 1974). Differences in base number are accompanied by strong size differences in the chromosomes.

The present note substantiates the cytological differences between these two families, with the report of $n = 8$ in the monotypic *Piptocalyx*, the only other genus of Trimeniaceae, confirming the initial observations on the cytology of the family. Cytological data provide convincing supportive evidence that *Xymalos* does not belong to Trimeniaceae, and it seems well placed in the Monimiaceae alliance.

Due to the cytological difficulties in the available material of *Xymalos*, a more accurate count proved impossible. We are thus unable at present to say whether chromosome number indicates close affinity to Monimiaceae s.s. ($x = 19$) or to Siparunaceae or Atherospermataceae (both $x = 22$). Morphology, however, does not indicate any affinity of *Xymalos* to the latter two families.

We thank T. Müller, National Herbarium, Salisbury, Zimbabwe-Rhodesia for providing the material of *Xymalos monospora* used in the study.

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NOTES ON THE FLOWERING AND LIFE HISTORY OF *NEUROLEPIS PITTIERI* (GRAMINEAE, BAMBUSOIDEAE)

The flowering and fruiting of bamboos has always attracted the attention of botanists and other interested observers because many species exhibit synchronous flowering and fruiting, followed by the death of the parent plants and re-establishment of the population from seedlings. Such life cycles may vary from 3–120 years, depending on the species (Janzen, 1976). Both McClure (1966) and Janzen (1976) in reviews of the reproductive behavior of bamboos stressed the need for detailed observations through several cycles from known populations in order to obtain accurate life histories of these plants.

Although the following notes on *Neurolepis pittieri* McClure are very fragmentary, we feel that they are important initial observations on the life history of this fascinating bamboo. More importantly, we hope it arouses the interest of persons better placed to make the necessary long-term observations needed to fully understand its life history.

Neurolepis pittieri has been reported to be endemic to the state of Aragua, Venezuela (Soderstrom, 1969), but more recent collections determined by Soderstrom extend the range of the species to Pico Phelps in southernmost Venezuela and Cerro Hornito, Chiriquí, Panama, the first Central American record for the genus. The population on which the present observations were made occurs in the Parque Nacional Henri Pittier (Rancho Grande), coastal cordillera, Aragua. It grows in cloud forest along a well-established trail at the place known as Cumbre de Rancho Grande at 1,450 m. It forms, at least locally, the dominant element of the herbaceous understory of the cloud forest.

Because of its greatly elongated blades and unbranched (above the base) culms, it is one of the most grasslike of the bamboos in general aspect (Fig. 1). Including its long blades, the plants grow 1–3 m tall vegetatively. When flowering, only single terminal inflorescences are produced on each culm, making the plants up to 4 m tall.

Huber observed the synchronous flowering of this population 12 July 1978 [*Huber 2162* (MO, VEN)]. Davidse, Huber, and B. Rollet (FAO) visited the population 17 April 1979 [*Davidse, Huber & Rollet 16634* (MO, VEN)]. At this time we observed only four mature flowering plants, from an original population estimated to consist of more than 100 plants. This last remnant of the 1978 flowering population probably represented plants that flowered slightly out of sequence compared to the majority of the other plants. One of the four was senescent and obviously ready to die. All of the other plants observed to be flowering in 1978 had died and for most of them only the remains of the rhizomes and sometimes a short portion of a culm could be seen. Close examination showed these rhizome systems to be completely dead, but, because of their greater woodiness, the rhizomes were decaying more slowly than the inflorescences, leaves, and upper portions of the culms. A few plants with the entire flowering culms still intact, but completely dead, were also observed. Seedlings abounded everywhere, ranging in size from recently germinated plantlets just a few centimeters

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FIGURE 1. Vegetative plant of *Neurolepis pittieri* in cloud forest in Parque Nacional Henri Pittier (Rancho Grande), Venezuela. Rod used as a scale is 2 m long.

tall to well-established plants 50–60 cm tall. Previously, Pittier, cited by McClure (1942: 183), had already noted that plants from the type locality between Colonia Tovar and El Lagunazo, also in the coastal cordillera in Aragua, died upon flowering; however, no other observations were recorded by him. Similar observations have been made on the Panamanian population (B. Hammel, pers. comm.). Flowering was first observed on 27 December 1977 [*Folsom, Dressler & Channell 7242* (MO)] and was later observed to approach its peak during March by Dressler. The population was revisited on 15 February 1979 [*Hammel 6207* (MO)] at which time a few plants were still in flower but most had died. Numerous seedlings had become established.

All observations demonstrate that this species flowers and fruits synchronously, dies, and regenerates itself from seed. How closely various populations

throughout the range of the species may be synchronized in their flowering is impossible to tell presently with our current meager data.

Just how long the entire life cycle may be cannot be stated conclusively, but we have incomplete data that it may be five years. This is deduced from the following facts. Huber and P. Berry (Missouri Botanical Garden) observed the Rancho Grande plants 30 August 1975. Most of the plants were vegetative, but a few old flowering plants were seen and a voucher was collected [*Berry 1161* (MO)]. This stage presumably represented one somewhat later than that observed in 1979. Apparently, in 1975 a few plants also flowered later than the majority of the plants in the population, and the vegetative plants probably represented vigorous young plants, at least several months older than the seedlings observed in 1979. Further observations by Huber in October 1975, January 1976 (Fig. 1), and October 1976, showed only vegetative plants. No further observations were made until flowering took place in July 1978, but it is assumed that the entire population remained vegetative during the intervening time.

Because *Neurolepis pittieri* in Rancho Grande is in an undisturbed, well-protected environment, is easily accessible, and apparently has a relatively short life cycle (for bamboos), it is hoped that complete observations of its life history and its interactions with other organisms can be made in the future. This could be a good test case for the predator satiation hypothesis proposed by Janzen (1976).

Fieldwork by Davidse was made possible by NSF grant INT 76-14750. We thank Dr. Thomas R. Soderstrom, Smithsonian Institution, for his determination of Panamanian collections of *Neurolepis*, and Mr. Barry Hammel for sharing his field observations with us.

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A NEW SPECIES OF *ALIBERTIA* (RUBIACEAE) FROM VENEZUELA

During the years 1977 and 1978, the Missouri Botanical Garden has collaborated with the Instituto Botánico of the Ministerio del Ambiente y de los Recursos Naturales Renovables of Venezuela in a joint program of botanical exploration to areas endangered by dam projects, drainage and river canalization plans, deforestation and agricultural activities, and other undertakings, all leading to drastic changes and destruction of the natural environment.

In a suite of Rubiaceae obtained from the Estado Apure of southwestern

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Venezuela by Dr. Gerrit Davidse and Mr. Angel C. González, the following new species of *Alibertia* was found and is herewith described.

Alibertia davidsae Steyermark, sp. nov.

Frutex 1–1.5 metralis, ramis superne dense pilosulis; foliis petiolatis, petiolis 5–15 mm longis dense pilosulis; laminis lanceolato- vel oblongo-ellipticis apice acutis obtusis vel rotundatis basi cuneatim acutis 6–11 cm longis 2.5–5 cm latis supra glabris subtus modice vel dense molliter pilosulis glabrescentibus, costa media pilis patentibus ad 0.5 mm longis munita, venulis tertiariis supra manifeste reticulato-elevatis subtus inconspicuis, nervis lateralibus utroque latere 8–9; petiolis 5–15 mm longis dense pilosulis; stipulis basi connatis 2.5 mm, lanceolatis acutis vel acuminatis 5–7 mm longis extus secus medium dense puberulis, alibi costatis cum marginibus costarum glabris; inflorescentia terminali sessile 13-flora; floribus masculinis: calyce valde campanulata 5 mm longa supra medium 4 mm lata leviter 5-denticulata dentibus late deltoideis acuminatis 0.1–1 mm longis intus glabris extus pilis patentibus munitis; corollis infundibuliformibus 9–17 mm longis, tubo 6–8 mm longo supra medium 3 mm lato intus dense tomentello praeter basin glabram 1 mm extus minute adpresso-puberulenti, lobis ovato-lanceolatis acutis 8.5–9 mm longis 3 mm latis extus minute adpresso-puberulentibus; antheris linearibus 6.5 mm. longis.

TYPE: VENEZUELA. ESTADO APURE: Distrito Pedro Camejo, 11 km E of Paso de San Pablo and 2 km ENE of Fundo Picachón along the banks of the Río Capanaparo, lat. 7°2′N, long. 67°39′W, 45 m, 8–9 May 1977, *Davidse & González 12910* (VEN, holotype; MO, isotype).

Paratypes: VENEZUELA. ESTADO APURE: Distrito Pedro Camejo, 22 km WNW of Paso de Cinaruco, along N bank of Río Cinaruco, lat. 6°34′N, long. 67°42′W, 60 m, 2 May 1977, *Davidse & González 12524*. 4 km NE of El Betun along banks of Río Capanaparo, lat. 6°58′N, long. 67°49′W, 10–11 May 1977, *Davidse & González 13016*. Banks of the Río Capanaparo between caños La Pica and La Guardia, 14 km SW of Urañon, lat. 6°54′N, long. 67°18′W, 35 m, 6–7 May 1977, *Davidse & González 12814*.

This riverine species is found in low gallery forest or savannas bordering streams in lowland terrain. It is related to *A. elliptica* (Cham.) Schum. and to *A. claviflora* Schum. From the latter it differs in the smaller staminate corollas, calyx, and anthers, shorter and narrower leaves, shorter stipules, and denticulate calyx. From the former it is distinguished by the much larger, longer-pointed, and differently shaped stipules which are more strongly pubescent, the longer petioles, the relatively longer and differently shaped leaves, the longer staminate corolla and calyx, and the densely pilosulous calyx.

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